Change in resilience of two coral reef communities over twenty five years: Influence of disturbance and other mechanisms

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DECLARATIONS

Statement of originality

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ABSTRACT

Mechanisms underlying the dynamics of two shallow coral reef communities at Lizard Island, Great Barrier Reef, Australia, over a twenty five year period (1981-2005 inclusive) were investigated using time series of photographs and a spatial model. At the first study site (sub-tidal, ~2 m depth) methods were developed to generate a spatial model based on local processes and disturbances. Rates for coral growth, mortality, recruitment and outcomes of pair-wise competitive interactions determined from the photographs were used to parameterise the model. Three acute disturbance events occurred at the site and determine the disturbance schedule of the model: 1982- a combination of coral bleaching and crown-of-thorns starfish; 1990 - cyclone waves; and 1996 - crown-of-thorns starfish.

Predicted coral community trajectories at the first site were not sensitive to the outcomes of competitive interactions, probably due to the high proportion of substratum not covered by coral (average 68%) and strong vertical separation among established corals), or to major changes in recruitment rates. The model trajectory accurately matched the observed trajectory until the 1996 disturbance, but only if coral mortality was confined to the three years of acute disturbance. Beyond that date (1997-2003), when the observed community failed to recover, it was necessary to introduce annual background mortality to obtain a good match between modelled and observed coral cover. This qualitative switch in the model may reflect a loss of resilience in the real community. Simulated over a century, an 8 year disturbance frequency most closely reproduced the mean community composition observed in the field prior to major disturbance.

At the second site (inter-tidal) a second spatial model was generated based on rates of coral growth, mortality, recruitment and outcomes of pair-wise competitive interactions measured at that site. The disturbance schedule (duration, timing and impact of disturbance events) varied between sites and illustrates how the manifestation of reef-wide disturbances (namely bleaching, crown-of-thorns starfish and cyclones) was highly variable at small spatial scales. Three putative causes of disturbance were as follow at the site: 1982 to 1989 - a combination of coral bleaching

and crown-of-thorns starfish; 1990 to 1992 cyclone damage / structural weakening; and 1996 to 1999 - crown-of-thorns starfish.

While coral species represented at the two sites (separated by several kilometres) were similar, their starting states and 25 year trajectories describing temporal change in community structure were very different. Obtaining a reasonable fit of the model to observed trajectories, required inclusion of site-specific disturbance schedules that reflected local site-specific variations in shelter and depth. Manipulation of the model revealed that differences in disturbance schedule between sites were more important than differences in growth, recruitment or interaction outcomes in driving community dynamics. Importantly, despite differences in disturbance schedules and community dynamics, the model indicates a qualitative switch from acute to chronic disturbance around the turn of the century, which is independent of local community structure and site-specific disturbance schedules.

Statement of co-authorship

The following people and institutions contributed to the publication of the work (Chapter 2 and 3) undertaken as part of this thesis:

Paper 1 *Mary Wakeford (70%), Craig Johnson (15%), Terry Done (15%)*

Paper 2 *Mary Wakeford (70%), Terry Done (20%), Craig Johnson (10%)*

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Author 1 and author 2 were the supervisors of this Master project, namely Dr Terry Done (Australian Institute of Marine Science) and Prof Craig Johnson (University of Tasmania). In all instances the candidate had the primary responsibility however, the co-authors contributed to the experimental design and implementation of the research program, data analysis, interpretation of results and manuscript preparation.

We the undersigned agree with the above stated ~~"p~~roportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

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CHAPTER 1

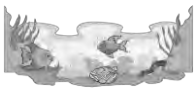
GENERAL INTRODUCTION

The dynamics of biological systems can be greatly influenced by the spatial attributes of habitat and the life history traits of individuals occupying it (Johnson 1997). Organisms are typically distributed non-randomly in space and, in sessile marine organisms, this feature is initially a consequence of the patchy distribution of larvae in the plankton (dependent upon the composition of reproductive individuals), small-scale hydrodynamics, and the colonisation behaviour of larvae (Keough 1983). The collective spatial arrangement of settled species will affect individual prospects for survivorship, growth and competitive interactions which, accordingly, will influence community dynamics. In sessile marine organisms much importance is placed on the intense local competition for space that occurs among immediate neighbours and the strong differences that arise in competitive ability (Sevens 1986; Buss 1990). While definitions of ‗community ecology' generally emphasise interactions among and within species (and competition in particular), the relative importance of these interactions compared with the independent responses to the environment and disturbances needs to be established. This is particularly true in today's world of climate change and other anthropogenic influences, where influences from the external environment may override or diminish the importance of intrinsic structuring processes such as recruitment patterns and competitive hierarchies.

This thesis investigates these issues in relation to coral community dynamics. The study's goals were to understand the ecological processes that drive community trajectories, to identify ―normal" fluctuations in community structure and deviations from them, and to gain insights into the underlying community dynamics, including differences between the sites, using a spatial model.

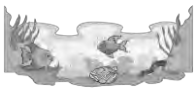
Community ecology

Life history traits of organisms play a central role in their ecology and evolution (Stearns 1976) and important processes affecting the structure and dynamics of biological communities include disturbance, predation, competition and disease (Hughes 1985). For sessile benthic organism



such as scleractinian corals (Cnidaria, Anthozoa, Scleractinia), dispersal of larvae and ecological connectivity between reefs as a result of larval dispersal are fundamental to maintaining populations and determining patterns of settlement (Harrison and Wallace 1990; Harrison and Booth 2007). At the time of recruitment, availability of suitable substrate on which to settle may be limited by sediment accumulation, competitors or other environmental factors. After corals settle and grow these same factors continue to influence community dynamics in addition to disturbance, predation, and disease. Other considerations specific to clonal organisms which may be heightened during periods of disturbance include the processes of fusion and fission, which add complexity to predicting population structure as a consequence of partial mortality, splitting and joining of colonies and seeding through fragmentation or polyp bail-out (Highsmith 1982; Sammarco 1982; Richmond and Hunter 1990). In addition, the fixed nature of sessile organisms means the ability to modify morphological structure in response to environmental factors (e.g. become more robust to withstand high wave energy) and to direct growth away from neighbours into open space and/or upper storeys (i.e. overtopping) are important strategies for survival and coexistence (i.e. interactions may also be facilitative). Issues such as degradation of water quality, disease or increased frequency and/or intensity of disturbance, interplay with community demographics and life history strategies to further affect community dynamics. The relative impact of processes structuring particular coral reefs (and other benthic communities) depends on their specific chronology, and may often be a function of seemingly remote, past events (Hughes 1985).

A myriad of processes can influence the structure of natural communities and the established concept has been to assume that ecological communities are inherently high-dimensional (Hutchinson 1957) and to build complex models incorporating as many ecological parameters and environmental factors as possible. An illustration of this is provided by the niche theory (Gause 1934; Hutchinson 1957; MacArthur and Levins 1967) in which each species persists because it is locally competitively superior in a niche defined by its biotic and abiotic environment. Hutchinson‘s ideas (1957) about fundamental and realized niches invoked competition to explain why species only occupy a subset of the niche space that would be suitable for them in the absence of competitors. This led to theories about community assembly

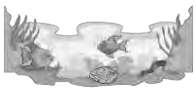


based on the competitive niche paradigm and became highly developed with the multispecies community matrix theory (Levins 1968). In due course, resource-based theory arose and recognised the importance of physiological and life history trade-offs (Tilman 1982, 1988; Kneital and Chase 2004) in shaping communities.

All these theories are finely tuned and focus on interspecific interactions and a multitude of other processes that may better inform us of the complexities of ecological communities but may also detract from developing any predictive theory (Chave 2003). Hubbell's neutral theory (Hubbell 1997, 2001) adopts a fundamentally different strategy and begins with the simplest hypothesis – for example, the functional equivalence of species – and then adds complexity back into the theory as required to fit the data. Functional equivalence is the cornerstone of the neutral theory and states that trophically similar species are approximately demographically identical on a per capita basis in terms of their vital rates of birth, death, dispersal and even speciation (Hubbell 2001, 2005). Although neutral theory may fail to capture the complexity of ecological communities (Alonso et al. 2006), it does surprisingly well given that it aims to use the minimum set of processes to satisfactorily explain an observed phenomenon.

Coral reefs, disturbance and alternate stable states

Coral reefs are dynamic systems that have evolved within a spectrum of disturbances throughout their geological history. Disturbance plays a significant role in determining community dynamics and structure (Connell 1978; Huston 1985) and at an intermediate level has been suggested as important in maintaining high species diversity on reefs by interrupting and setting back the process of competitive elimination, or by removing occupants that are competitively excluding further invaders (Connell 1978). Much research has focussed on whether, following a disturbance, hard corals recover to approximate the communities that existed prior to disturbance (Pearson 1981; Connell 1997) or whether there is a shift to an alternative state dominated by macro-algae, soft corals, or ~~b~~barren" grounds characterised by coralline and filamentous algae (Done 1992; Hughes 1994; Knowlton 1992; Wooldridge et al. 2005). Evidence suggests that coral reefs are dynamic systems with multiple stable states (Done 1992; Knowlton 1992; Mumby et al. 2007) and their ability to return to the state prior to disturbance cannot be taken for granted

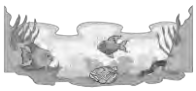


(Connell 1997; Kinizie 1999; Graham et al. 2006). This is especially true in recent times, as reefs are under increased pressure, ranging from local and regional disturbances (over-fishing, water quality degradation, predatory sea-stars and cyclones) to global disturbances associated with climate change (bleaching, disease and ocean acidification). A ~~"p~~hase shift" refers to a significant change in community structure and composition to an alternative state (e.g. from coral to algal dominance) which, if stable (i.e., alternative stable state), is referred to as a ~~"re~~gime shift" (Nyström et al. 2000). Such regime shifts have been reported on reefs from around the world (Done 1992; Wilkinson 1999) and can be long-lasting and difficult to reverse (Hoegh-Guldberg et al. 2007).

Ecological resilience and resistance

The concepts of resilience and resistance have been developed to describe the complex dynamics of ecosystems and communities in response to disturbance. Ecosystem *resilience* refers to the ability of a community to absorb shock, resist phase shifts and regenerate after natural and human-induced disturbances (Nyström et al. 2000; Bellwood et al. 2004). It expresses the ease or difficulty with which a system can switch between alternative stable states, with more ~~"re~~silient" systems having higher barriers to switching (Ives and Carpenter 2007). It recognises the potential existence of critical tipping points (*thresholds*) that when crossed may cause a shift to an alternative stable state, which is maintained by self-reinforcing feedback mechanisms that tend to keep the ecosystem in its new state (Knowlton 1992; Nyström et al. 2008). Being able to determine the ecological thresholds of a system and assessing when they are being approached is complex, and the application of these concepts to environmental management has been limited (Connell and Sousa 1983; Scheffer et al. 2001; Groffman et al. 2006). The difficulty or ease of changing an ecosystem is determined by the *resistance* of the system (Pimm 1984) and may be related to ~~"in~~trinsic" (e.g. species specific) and ~~"e~~xtrinsic" (i.e. environmental) factors of the community that may, for example, give individual corals or communities the ability to resist bleaching or to survive after being bleached (e.g. Done 1999; West and Salm 2003).

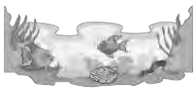
Given predictions that the frequency and intensity of disturbances affecting coral reefs will continue to increase (Hoegh-Guldberg 1999; Kleypas et al 1999; Hughes et al 2003), the



implications for community structure and growth of reefs are potentially profound. Community shift to a non-reef-building state for extended periods of time (decades to centuries) has major implications for reef maintenance and growth as well as the continued support of associated biological assemblages (e.g. site attached fish and motile invertebrates). Coral reefs are complex ecological systems in which the living organisms contribute to the non-living physical structure through centuries of ecological engineering and sedimentary accumulation (Done, in press). For reefs to persist as substantial physical structures, accumulation of reef material needs to exceed cumulative loss (through biological and physical erosion), and factors that decrease growth and reproduction of corals or increase mortality of corals have the potential to tip the balance toward inexorable reef decline (Knowlton and Jackson 2008).

Temporal change and future predictions

Interpreting temporal change in a community is critical in distinguishing between shifts in community composition attributable to "natural" fluctuations with otherwise stable long-term dynamics, and those reflecting some kind of fundamental change in the underlying dynamics (Rand and Wilson 1995; Johnson 2009). Characteristics of coral reefs that make predicting their behaviour difficult include intrinsic dynamism, non-linear behaviour, critical tipping points and multiple stable states (e.g. Done 1992; Knowlton 1992; Mumby et al. 2007; Nyström et al. 2008). A fundamental change, such as a shift in disturbance regime, can have considerable long-term consequences for community structure and dynamics but may be difficult to detect. Historical baselines and long-term ecological studies (Connell 1997) are essential resources for interpreting community change over ecological time scales (years to centuries), and provide insight into the interplay between disturbance and local ecological processes, both present and past (Hughes 1989). Research that goes beyond routine monitoring and mapping is required to unravel processes driving dynamics, to identify phase shifts to alternative stable states associated with loss of resilience, and to develop meaningful predictive models. Understanding of this behaviour is evolving, as is the task of policy makers and managers in providing insurance against unforseen ecosystem responses in the face of environmental change (Nyström et al. 2008). "Adaptive management" is a tool for approaching environmental problems where solutions to

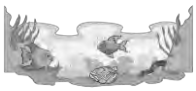


problems are proposed and implemented, but prescriptions are constantly re-evaluated based on actual ecosystem response to management (Holling 1978; Walter 1986; Groffman et al 2006). Empirical research that identifies ecological thresholds of communities and whether they are being approached would greatly advance these types of management strategies.

Thesis overview

In 1979-80, T. Done established a long term study comprising 30 permanent photographic sites on the Great Barrier Reef to document fine-scale temporal variability in a range of habitats. This thesis investigates change in coral community dynamics at two reef-top sites over a 25 year period. Both differences and similarities in the response of the coral communities at the sites to disturbance are investigated, in particular changes through time as a consequence of disturbance (e.g. cyclones, crown-of-thorns infestation, bleaching), variability in growth and recruitment, and the outcomes of interactions among component individuals. Key issues investigated in this study are to determine 1) which ecological processes are most important in driving the community trajectories at each site, 2) whether it is possible to discern "normal" changes that are part of the usual dynamics/fluctuations of a reef community structure, from changes that represent some kind of fundamental shift in underlying dynamics (which may lead to long-term change in community function), and 3) whether local biological and physical factors may influence the impact of disturbance at small spatial scales.

Field observations of ecological parameters were derived from the photographs and used to develop models reproducing the actual community trajectories. Through manipulation of model parameters the key drivers of community dynamics are investigated and differences between sites inform the development of a conceptual model to identify both the contrasting drivers of change at the two sites and similarities in gross dynamics. Time periods where parameters need to be altered to achieve a reasonable fit between predicted and actual trajectories are suggestive of some kind of fundamental shift in the system. Methods used in this thesis to interpret temporal change and shifts in community dynamics are supportive of techniques aimed at determining the characteristic length scales of ecological systems (Keeling et al. 1997; Pascual and Levin 1999). These techniques have potential in a decision support role in determining scales for monitoring,



interpreting whether change in community structure reflects a shift in underlying dynamics, and determining interactions among species in complex ecological systems (see Habeeb et al. 2007; Johnson 1997 and 2009).

Devising methods that will quantify reef resilience and identify thresholds are complicated due to the myriad of processes operating at a range of scales in time and space, and because complex interactions between different processes may arise (Johnson 2009). To progress understanding in these areas it is crucial to consider emerging theories and ideas that may challenge or fundamentally change many basic predictions of ecological theory. For example, many ecologists have worked on the importance of competition, predation, physical disturbance and physiological stress in structuring communities, however many species interactions are indirect and/or facilitative (i.e. positive) (Bruno et al. 2003), contrary to the conventional negative expression of competition outcome. Emerging theories and processes may ultimately lead to a more accurate and inclusive understanding of natural communities (Bruno et al. 2003). This in turn should lead to improved predictive modelling of complex natural systems, among which coral reefs are a supreme example.

CHAPTER 2

DECADAL TRENDS IN A CORAL COMMUNITY AND EVIDENCE OF CHANGED DISTURBANCE REGIME

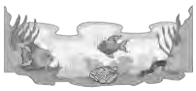
Research for this chapter has been published as:

Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs* 27:1-13

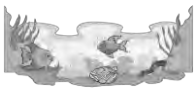
Contributions: Wakeford 70%; Johnson 15%; Done 15%.

Abstract

A twenty-three year data set (1981 – 2003 inclusive) and the spatially explicit individual-based model _Compete‘© were used to investigate the implications of changing disturbance frequency on cover and taxonomic composition of a shallow coral community at Lizard Island, Australia. Near-vertical *in situ* stereo-photography was used to estimate rates of coral growth, mortality, recruitment and outcomes of pair-wise competitive interactions for 17 physiognomic groups of hard and soft corals. These data were used to parameterize the model, and to quantify impacts of three acute disturbance events that caused significant coral mortality: 1982- a combination of coral bleaching and crown-of-thorns starfish; 1990 - cyclone waves; and 1996 - Crown-of-Thorns starfish. Predicted coral community trajectories were not sensitive to the outcomes of competitive interactions (probably due to the high proportion of substratum not covered by coral (average 68%) and strong vertical separation among established corals) or to major changes in recruitment rates. The model trajectory of coral cover matched the observed trajectory accurately until the 1996 disturbance, but only if all coral mortality was confined to the three years of acute disturbance. Beyond that date (1997-2003), when the observed community failed to recover, it was necessary to introduce annual chronic background mortality to obtain a good match between modelled and observed coral cover. This qualitative switch in the model may reflect actual loss of resilience in the real community. Simulated over a century, an 8 year disturbance frequency most closely reproduced the mean community composition observed in the field prior to major



disturbance events. Shorter intervals between disturbances led to reduced presence of the dominant hard coral groups, and a gradual increase in the slow growing, more resilient soft corals, while longer intervals (up to 16 years) resulted in monopolization by the fastest growing table coral, *Acropora hyacinthus*.

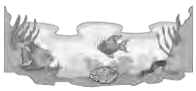


Introduction

Coral reefs are among the world's ecosystems most at risk from global change, both climate related and from direct pressures of human over-exploitation and pollution (Kinzie and Buddemeier 1996; Hoegh-Guldberg 1999; Kleypas et al. 1999; Hughes et al. 2003). Events that kill extensive areas of coral reefs are increasing in frequency and intensity and include coral bleaching (Hoegh-Guldberg 1999; Kleypas et al. 1999), outbreaks of coral-eating predators (Seymour and Bradbury 1999) and disease (Harvell et al. 2002; Rosenberg and Ben-Haim 2002). In addition, deteriorating coastal water quality can also threaten reef health (Wilkinson 1999; McCulloch et al. 2003).

Coral reefs have evolved within this spectrum of disturbances, with variation in the type, scale, intensity and frequency of disturbance all playing a major role in determining community dynamics and structure (Connell 1978; Huston 1985). Much research has focussed on the response of reefs to disturbance, and in particular whether hard corals recover to approximate the communities that existed prior to disturbance (Pearson 1981; Connell 1997) or whether there is a switch to alternative states dominated by macro-algae, soft corals, or _barren' grounds characterised by coralline and filamentous algae (Done 1992; Hughes 1994; Knowlton 1992; Wooldridge et al. 2005). Scientists predict a continued increase in disturbance frequency with dire consequences for coral reefs (Hoegh-Guldberg 1999; Kleypas et al. 1999; Hughes et al. 2003). It is predicted that most coral reef systems will be experiencing near-annual bleaching events that will exceed the extent of the 1998 bleaching event by the year 2040 (Hoegh-Guldberg 1999). However, a detailed understanding of how coral reefs might respond to changing patterns of coral mortality is unclear.

An indication of likely future changes in coral reefs under altered environmental conditions and disturbance regimes may be gained by investigating changes in the recent past. In particular, it would be valuable to understand past variability in the trajectories of coral cover and composition, and to understand the relative roles of key ecological processes, such as recruitment, growth, survivorship and competition, in driving that variability. In this study, a



coupled-lattice model of an area of reef was built and tuned to closely match the observed trajectory of the study area in the period 1981 – 2003. This provided a basis to understand the role of the various ecological and disturbance processes in structuring the community, and to investigate possible futures for this area in coming decades.

Throughout the lives of corals, there can be significant physical contact and competition for space on the reef. Outcomes of competition can be important in determining the survival of individual corals (Tanner et al. 1994; Sheppard 1985). Dunstan and Johnson (2005) successfully modelled marine epibenthic community trajectories based on the probability distributions describing outcomes of pair-wise competitive interactions, recruitment, mortality and growth rates. This study explores how these same processes have played out (1981-2003), and might shape coral community dynamics in the future (2003 – 2103), in a 32 m^2 area monitored photographically. Processes that play a key role in structuring communities at one time may become less important once disturbance becomes more frequent, leading to lower benthic cover and reduced likelihood of interaction among established colonies than in more crowded sites, and greater availability of space for growth and new colonisation. The study area experienced three major disturbance events in the period 1981-2003. In 1982 there was significant coral mortality from a combination of coral bleaching and crown-of-thorns starfish (Harriott 1985), in 1990 corals were damaged or removed entirely by waves from Cyclone Ivor (van Woesik et al. 1991) while in 1996 corals were significantly affected by predation from crown-of-thorns starfish (Sweatman et al. 1998; Pratchett 2005).

The particular aims of the study were to determine 1) whether local ecological processes affecting corals can be modelled to produce a community trajectory similar to the observed community over 23 years; 2) which processes are most important in determining the trajectory; and 3) the range of variability in predicted trajectories of the modelled community under various disturbance intervals over 100 years.

Materials and methods

Study site

The study site is at Lizard Island on the Great Barrier Reef, Australia, 30 km off the north Queensland coast. It is a mid-shelf continental island beyond the reach of river flood plumes, and has been protected as a no-take zone since 1983 (Great Barrier Reef Marine Park Authority 1983). The island has extensive fringing reefs and a large, well-developed lagoonal area. The study site (4 m x 8 m) is located on the southeast fore-reef flat that extends from Bird Islet to South Island (Fig. 2.1a). It represents a small section of the fore-reef at a depth of approximately 2.5 m below extreme low tide and is regularly subjected to strong surge.

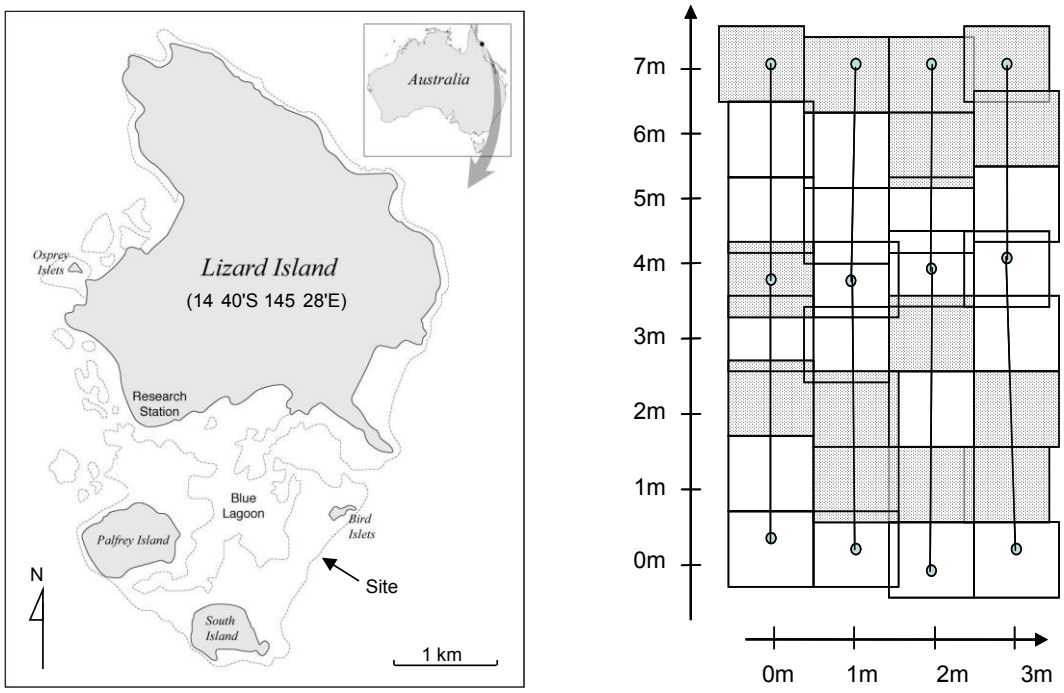


Fig 2.1 Lizard Island study site. **a** Location map. **b** Details of study site. Rectangles represent areas photographed with 35 mm slides, dots represent steel pegs driven into the reef and lines connecting them are tape measures laid during photography. Shaded rectangles represent the subset of slides analysed using photogrammetry software to derive data for rates of growth, recruitment, mortality and interaction outcomes.

The substratum (Fig. 2.2a) is a continuous limestone pavement, relatively sediment-free, and with hard corals comprising plating and corymbose *Acropora*, bushy *Pocillopora*, small colonies of

faviids and massive *Porites*, and soft corals from the family Alcyoniidae. This community type is fairly typical for the south-east fore-reef flat at Lizard Island, and although findings from this study site may be similar for other places on the reef, it would be necessary to expand the sampling protocol to include replicate sites to make such inferences. Additional sites (four) have been established in a range of habitats around Lizard Island and will be investigated at a later date to expand the scope of this study.

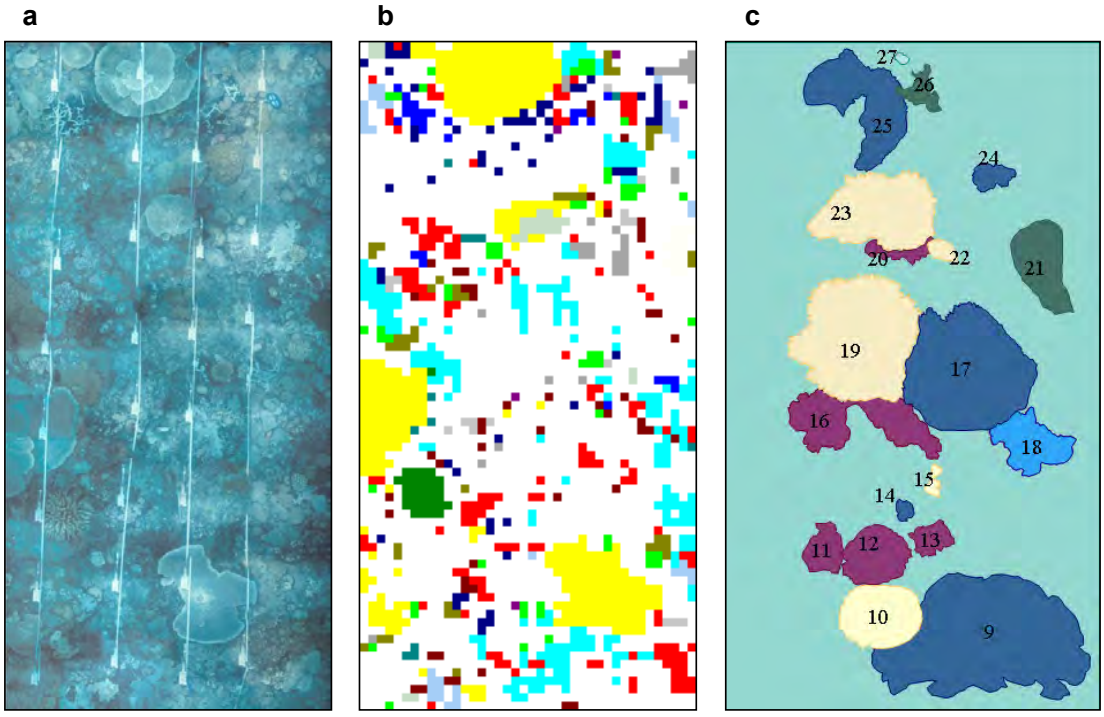
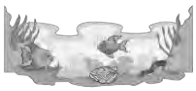


Fig. 2.2 Lizard Island study site. **a** Photo mosaic of 32 images comprising the site in 1981, approximate area 4 m x 8 m. **b** Base map in Compete© derived from point sampling of a. **c** Detail of colony outlines generated using Intergraph ImageStation© photogrammetry software.

Sampling

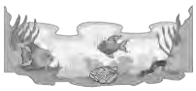
The benthic community within the study site was monitored most years using near-vertical stereo photography (see Done 1981). Photographs were taken on Kodachrome 64 slide film from ~2 m above the substratum at 1 m intervals along tape measures stretched between steel pegs within the site (Fig. 2.1b) using two Nikonos cameras fitted with 28 mm lenses and mounted 300 mm apart on a rigid aluminium frame. A 1.9 m rod with scale object and spirit levels fitted at right angles was used to acquire overlapping stereo pairs of the entire site in 16 of the 23 years



between 1981 and 2003 (Fig. 2.2a). The photographic slides were digitised (file size ~27 MB) and analysed using two methods: 1) a point sampling method to map and quantify changes in community structure based on empirical data, and 2) stereo observation and photogrammetry to quantify rates of growth, mortality, recruitment and outcomes of inter-specific interactions to generate a model. In the point sampling, each image pair (32 pairs per year) was viewed stereoscopically and the benthos underlying a 10 x 10 grid of evenly spaced points was identified to the highest possible taxonomic level before assigning it to one of 17 physiognomic groups. This procedure provided an estimate of percentage cover of each physiognomic group through time (the ‗observed' trajectories) and also a base map for the spatial model (1981 only). For the base map, the observed benthic attribute at each point was assumed to fully occupy a 10 x 10 cm square (Fig. 2.2b). Stereo observation and photogrammetry were then used to provide estimates of growth, mortality, recruitment and outcomes of inter-specific interactions for each physiognomic group. Images were displayed on a flat monitor using photogrammetry software (Intergraph ImageStation© Stereo Softcopy Kit, see http://www.intergraph.com), viewed through liquid crystal shutter eyewear (Stereographics CE-3), and mapped on-screen using a mouse-driven cursor. The time-series of colony sizes and status (live, dead, injured) were then used to compute parameter rates for recruitment, growth, mortality and pair-wise interaction outcomes to be used in the spatial model ‗Compete©' (available at http://www.zoo.utas.edu.au/CJPblist/Compete%20program/).

Modelling the community trajectory

The 8 m x 4 m base map of the1981 coral community was represented on a spatial landscape of 320 x 160 cells, with each cell representing a real area of 25 x 25 mm on the reef. The ‗Compete©' model was then run on the landscape for either 23 or 100 years at time steps of one month. Compete© uses a probabilistic (stochastic) cellular automaton as its kernel, with growth, mortality, recruitment and disturbance expressed as conditional probabilities of cell occupancy and at each time-step. The terms ‗site' and ‗model' are used below to distinguish between the empirical data (from photographs) and the modelled outputs.

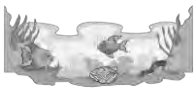


At the site, measurements for *growth* were derived for each physiognomic group from annual change in colony area (until the colony died or reached 2003). Growth was converted from change in area to a rate of linear extension (based on change in equivalent circle diameter) to a monthly probability of growth into an empty cell. Average and variable growth were trialled in the model. Compete© models variable growth rate by assigning new recruits a growth rate selected randomly from a given range of growth rates. This range was defined as the average growth ±1 standard deviation of colonies measured at the site.

Mortality in a given physiognomic group was defined in the model by (i) the probability of mortality for that group, which applied to every cell of that group in each time-step; and (ii) the size of the mortality event, which defined the maximum number of contiguous cells of the same group that were removed in a single mortality event. At the site, the probability of mortality (i) was derived from the number of *whole colonies* dying per year for each group. The size of the mortality event (ii) was set to the average size of colonies that died across all groups (the model does not allow for different size mortality events to be set for each group). Therefore, to account for differences in the size of the mortality events among groups, a correction factor was applied to mortality probability. For example, if the size of the mortality event for a given group was only half as big as the set mortality size, its mortality probability was halved.

Recruitment occurred only in empty cells on the landscape and was set to ‗open' whereby recruitment did not depend on the relative abundance of physiognomic groups on the current landscape. Instead, a group was selected at random from any that had existed in the system, and it recruited to the empty cell with a probability defined by its recruitment rate. At the site, recruitment rate for each group was estimated by converting the average number of recruits/yr/area to the monthly probability (0-1) that a group would recruit to an unoccupied cell on the model landscape.

Outcome of interactions between each pair of physiognomic groups was assessed at the site and converted to a probability of win, loss or stand-off (standoff was assigned to corals in very close proximity to one another (usually margins touching) where both corals existed without obvious



detrimental effects, such as shrinkage or die-back at touching margin). In the model, if a central cell was occupied by a group *Y*, then a neighbouring cell *X* was chosen at random, and group *X* overgrew group *Y* (the central cell) with probability $Pr_{XY}*G_{XY}$ where Pr_{XY} was the probability of *X* winning an encounter with *Y*, and G_{XY} was the growth rate of *X* over *Y*. All of the 136 possible pair-wise combinations among the 17 groups at the site were considered in deriving probabilities of win, loss or stand-off. However reasonable data (defined arbitrarily as $n \geq 8$ independent observations) were available for only 43 interactions. All other interactions were assigned equal probabilities of win, loss and standoff.

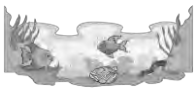
The period 1981-2003 was divided into 6 periods to distinguish between years of ~~"a~~cute disturbance" and ~~"i~~nter-disturbance" periods as follows:

1982 – coral bleaching and crown-of-thorns starfish (acute disturbance)
1983-1989 – inter-disturbance period 1
1990 – cyclone damage (acute disturbance)
1991-1995 – inter-disturbance period 2
1996 – crown-of-thorns starfish (acute disturbance)
1997-2003 – inter-disturbance period 3

The differing trajectories of each of these periods were simulated using 1) rates of growth, mortality and recruitment determined separately for each period, and 2) probabilities for outcomes of competitive interaction based on observations averaged over the 6 periods. The goodness of fit of the modelled to the observed trajectory of coral community structure was compared graphically. The best-fit trajectory was obtained by experimenting with combinations of average growth rate and variable growth rate (a random selection from a range defined by average ± 1 SD), and the presence or absence of 'background mortality'. These best-fit settings were then fixed for subsequent runs of the model, which investigated sensitivity to varying rates of recruitment and outcomes of interactions.

Effects of recruitment and interactions

For recruitment, the following scenarios were examined: 1) failed recruitment (all recruitment set to zero); 2) the observed mean recruitment rate across all physiognomic groups; 3) double the



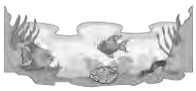
observed mean recruitment rate of each physiognomic group; and 4) ten-fold the observed recruitment rate of each physiognomic group. For competitive interactions, the observed interaction outcomes were compared with three arbitrary scenarios, namely, 1) equal probability of win, loss or standoff (outcomes as 33:33:34%), 2) 100% standoff (outcomes as 0:0:100%); and 3) randomly determined probabilities of win and loss, with no standoffs allowed (outcome as [win] + [loss] = 100%).

Effects of changed disturbance frequencies projected over 100 years

Effects of various disturbance intervals on the modelled community were simulated over a 100 year period, with disturbance fixed at regular intervals of 2, 4, 6, 8 and 16 years. Each disturbance was defined using the average of parameter rates determined for the three disturbance years (1982, 1990, 1996). All inter-disturbance periods were defined by the parameters averaged over all other years, except for background mortality, which was set to zero (see Results). The 1981 base map provided the starting spatial configuration, and the first disturbance occurred at year 1 in all cases followed by the requisite number of inter-disturbance years, i.e. for a 16 year disturbance frequency, 1 year disturbance followed by 15 years of inter-disturbance rates, repeated until reaching 100 years. Immediately prior to each disturbance the model community composition was recorded and compared to pre-disturbance communities from the observed trajectory (Jan 1981, 1989, 1994, 1995 and 2002).

Analyses to compare observed and model trajectories

Absolute percent cover data was generated for the observed (based on point-sampling empirical data) and model trajectories (based on parameter estimates input into Compete©) for each physiognomic group. These data were square-root transformed to down-weigh the importance of the highly abundant species, and a Bray-Curtis similarity matrix was generated among years. Changes in composition through time were followed using Kruskal's non-metric multidimensional scaling (NMDS) of the pre-disturbance abundances of each group. A Procrustes rotation analysis was used to assess the degree of concordance between the modelled trajectories and the observed trajectory. Procrustes analysis works by scaling, rotating and



dilating one ordination solution and then superimposing it on the second, maximising the fit between corresponding observations. The least-square criterion that minimizes the sum of the squared residuals (m^2) between two configurations was used; low values for m^2 indicate strong concordance (Gower 1971). „ProTest", which assesses the statistical significance of the Procrustean fit (Peres-Neto and Jackson 2001), was used with 9999 permutations to assess the significance of pair-wise comparisons of the trajectory for each disturbance interval against the observed trajectory.

The NMDS analysis was carried out using the package MASS in R version 2.4.1 (R Development Core Team 2005, see http://www.r-project.org/). The R package Vegan was used to calculate the Bray-Curtis distance measure, and to undertake the Procrustes and ProTest procedures. Primer 5 (Clarke and Warwick 2001) was used to generate plots of the 100 year NMDS trajectories.

Results

Observed changes in the study site

Cover of hard corals was ~26% when the site was first established in 1981, and was reduced greatly after each acute disturbance event (Fig. 2.3a). However, following the disturbances in 1982 and 1990, hard coral cover either regained (post-1982) or exceeded (post-1990) previous levels. In contrast, following the acute disturbance in 1996, recovery of hard corals was minimal and cover remained below 24% for the remainder of observations. Of the 17 physiognomic groups, fourteen were hard corals and three were soft corals from the family Alcyoniidae (Table 2.1). Among the hard corals, the compact bushy *Pocillopora damicornis* and the table coral *Acropora hyacinthus* were the most abundant. During inter-disturbance years *A. hyacinthus* overtopped all other physiognomic groups and quickly dominated cover (Fig. 2.3a). However it

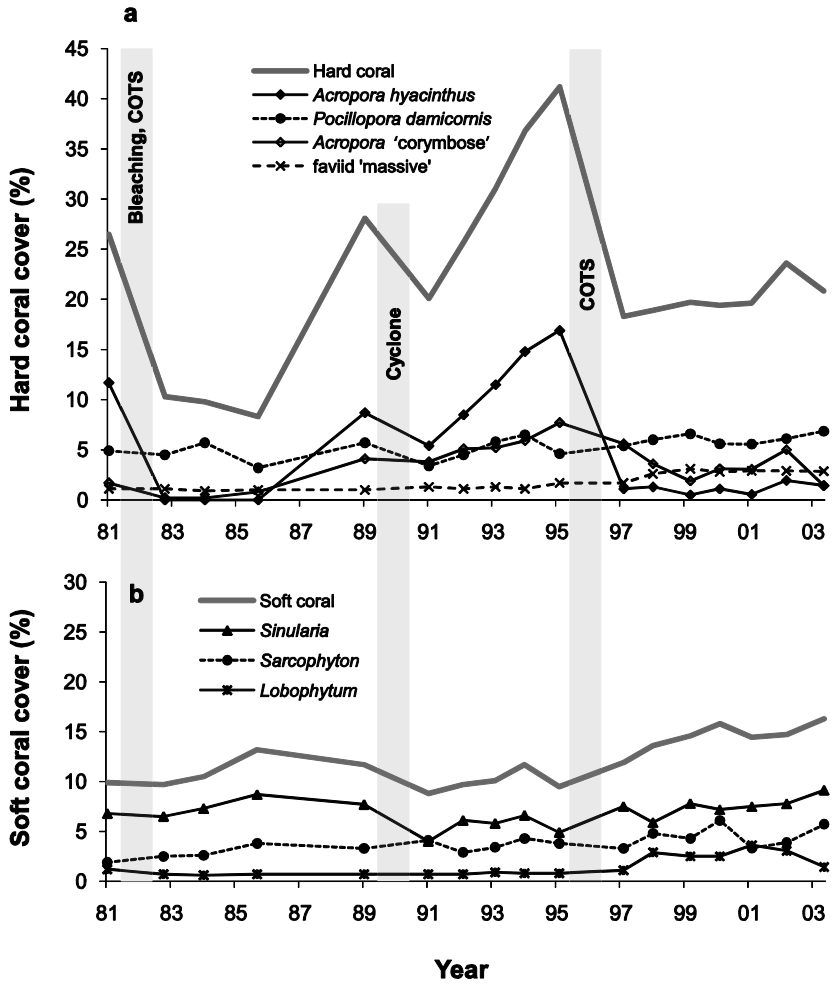
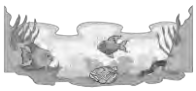


Fig. 2.3 Temporal patterns in cover of the most abundant corals at the study site, 1981-2003. **a** Hard corals. **b** Soft corals. *Vertical bars* identify discrete disturbance events.

was also the most susceptible to acute disturbance. Cover of the compact robust coral *Acropora* ‗corymbose' also fluctuated markedly but its cover did not attain that of *A. hyacinthus. P. damicornis* maintained fairly constant cover over the observation period as a result of moderate rates of growth, high recruitment and moderate-high mortality during both acute and inter-disturbance years (Fig. 2.4a-c). Massive faviids and *Porites* were slow growing, long-lived and had medium to high recruitment rates. Cover for both these groups remained stable but low throughout the period. Soft coral cover was only about one third that of hard coral and fluctuated independently of acute disturbance (Fig. 2.3b), apart perhaps from physical damage caused by cyclone-generated waves in 1990. Two of the three soft corals, *Sinularia* spp. and *Sarcophyton* spp., maintained a remarkably uniform cover and population size throughout the study. They had



relatively little turnover, moderate to low growth and moderate to high recruitment (Fig. 2.4a-c). *Sinularia* spp. had the highest average cover through time (6.9%) of all physiognomic groups.

Table 2.1 The 17 physiognomic groups showing mean percent cover for the period 1981-2003.

Physiognomic group by family	Average % cover	Minimum	Maximum	SE
Acroporidae				
Acropora hyacinthus	5.0	0.0	16.9	1.5
Acropora 'corymbose'	3.4	0.2	7.7	0.6
Acropora intermedia	1.5	0.0	4.4	0.4
Acropora millepora	0.5	0.0	1.1	0.1
Acropora humilis	0.4	0.0	1.1	0.1
Acropora gemmifera	0.4	0.0	0.8	0.1
Acropora cuneata	0.2	0.0	0.8	0.1
Acropora florida	0.2	0.0	0.6	0.1
Pocilloporidae				
Pocillopora damicornis	5.3	3.2	6.9	0.3
Pocillopora verrucosa	1.5	0.8	2.4	0.1
Pocillopora eydouxi	0.2	0.0	1.0	0.1
Faviidae				
Faviid „massive'	1.8	0.9	3.1	0.2
Faviid „encrusting'	0.2	0.0	0.4	0.0
Poritidae				
Porites „massive'	1.7	1.0	2.5	0.1
Alcyonidae (Soft corals)				
Sinularia spp.	6.9	4.0	9.1	0.4
Sarcophyton spp.	3.8	1.9	6.1	0.3
Lobophytum spp.	1.5	0.6	3.6	0.3

Growth

Mean growth rates ranged from negative values up to 50 mm increases in equivalent circular diameter per year (Fig. 2.4a). Five physiognomic groups had negative growth (due to partial mortality exceeding overall growth), and seven (including all soft corals) had faster mean growth during acute disturbances than inter-disturbance years. Seven of the eight fastest growing physiognomic groups were in the genus *Acropora*, and all of the ten most rapidly growing groups were either *Acropora* or *Pocillopora*. The massive and encrusting hard corals and the soft corals were the slowest growing groups.

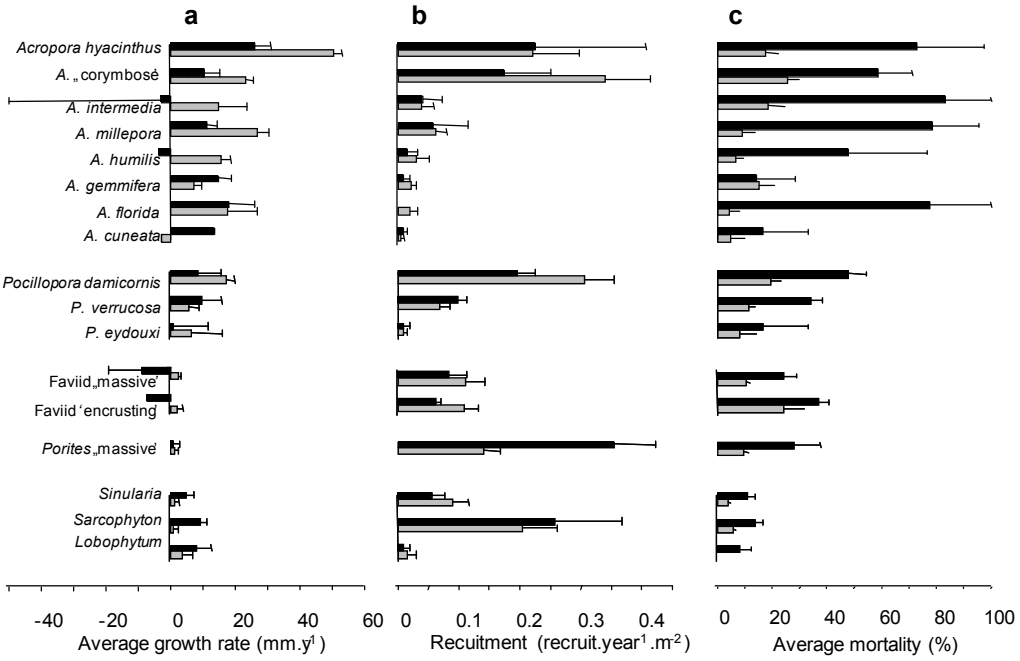
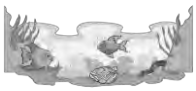


Fig. 2.4 Rates of growth, recruitment and mortality for 17 coral groups comparing "Acute disturbance" years (black bars) and "Inter-disturbance" years (grey bars). Error bars indicate standard error. **a** Mean Growth rates for each physiognomic group expressed as mm year^{-1} increase in equivalent circular diameter. **b** Mean annual recruitment for each physiognomic group. **c** Mean percentage of colonies that died annually for each physiognomic group.



Recruitment

Massive *Porites* had the highest recruitment rate and this occurred during acute disturbance years (Fig. 2.4b). In some cases, new *Porites* colonies only became visible in the images after upper storey *Acropora* species had died, making it hard to determine exactly when *Porites* recruitment had occurred. The 5 most abundant physiognomic groups had the five highest recruitment rates except for *Sinularia* spp. which was ninth highest. Recruitment for physiognomic groups ranged from <1 to 11 recruits per year over the study area (i.e. 32 m^2). The average total number of recruits (all groups combined) was 27 per year (which is equivalent to cover of < 0.02 m^2 or about 0.05% of the area of the site).

Mortality

During acute disturbance years, most physiognomic groups (16 out of 17) had higher mortality rates than in inter-disturbance years (Fig. 2.4c). During acute disturbances the fast growing and abundant *Acropora* species had the highest mortality with slower growing hard and soft corals having lower mortality. During inter-disturbance years, mortality was low and relatively even across all physiognomic groups.

Interactions

There were 3445 colony measurements taken of 843 individual colonies over the 16 sample periods. Of these colony measures, 2363 (68%) were recorded engaged in one or more interactions with another colony; 1986 were standoffs (84%) and 377 were win/loss interactions (16%) in which one of the contestants suffered a net reduction in area. Of 136 possible pair-wise interactions good data were obtained (i.e. n>=8) for 43 interactions (32%) of which 16 showed unambiguous outcomes (Fig. 2.5). The tabular coral *A. hyacinthus* was most successful in competitive interactions, including interactions with the second ranked *Acropora* ‗corymbose' and third ranked soft coral, *Sarcophyton* spp. The soft coral *Sinularia* spp. and massive *Porites* consistently lost to overtopping *Acropora*, whereas *P. damicornis* was most likely to be involved

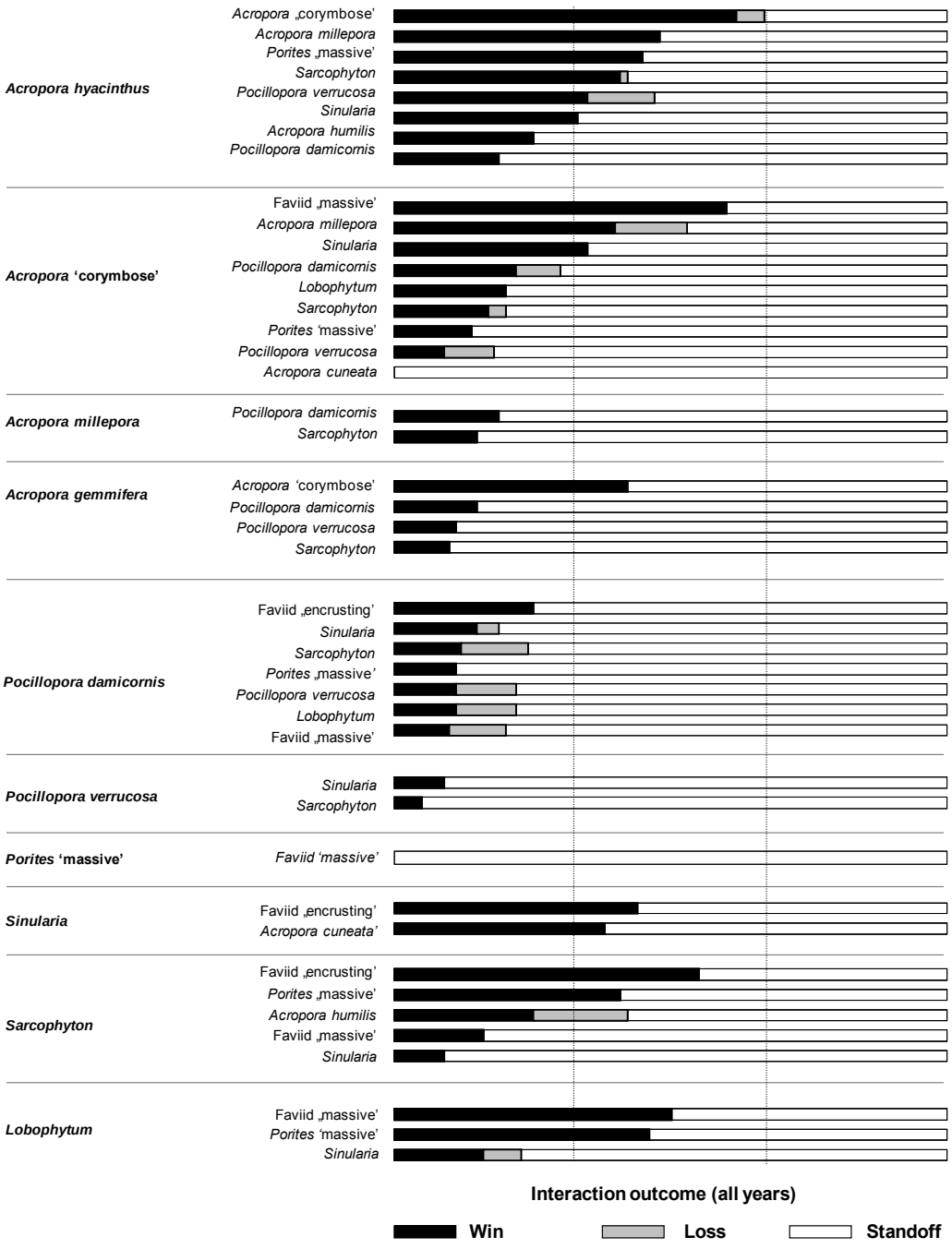


Fig. 2.5 Outcomes of interactions among 43 physiognomic groups. The graph shows the proportions of wins, losses and standoffs of the first-named physiognomic group (bold lettering) in interactions with the second.

in a stand-off interaction. These observations defined the probabilities of outcome of inter-specific interactions used in the modelling. Pair-wise combinations that occurred less than eight times (56 % of the possible number of pair-wise interactions) and thus were relatively rare during the study period were arbitrarily given equal probabilities of win, loss or standoff. Interactions

between *A. intermedia* and other physiognomic groups were usually observed as *A. intermedia* overtopping its competitor so that both colonies would co-exist, and in this case the outcome was set to standoff, i.e. 0:0:100% (12% of all observed pair-wise interactions).

Physiognomic groups rated by relative percentage

For each of the rates that indicate vigour – growth, survival (complement of mortality) and recruitment – a relative percentage from 0-100 was assigned for each physiognomic group (Fig. 2.6). For both recruitment and growth, relative percentage is defined as the physiognomic group rate / highest rate recorded *100, such that the highest percentage was 100. The five top rated physiognomic groups (combining growth, survival and recruitment) during inter-disturbance years were also the five most abundant groups by cover over the entire study period, apart from the most abundant, *Sinularia* spp. which was rated tenth.

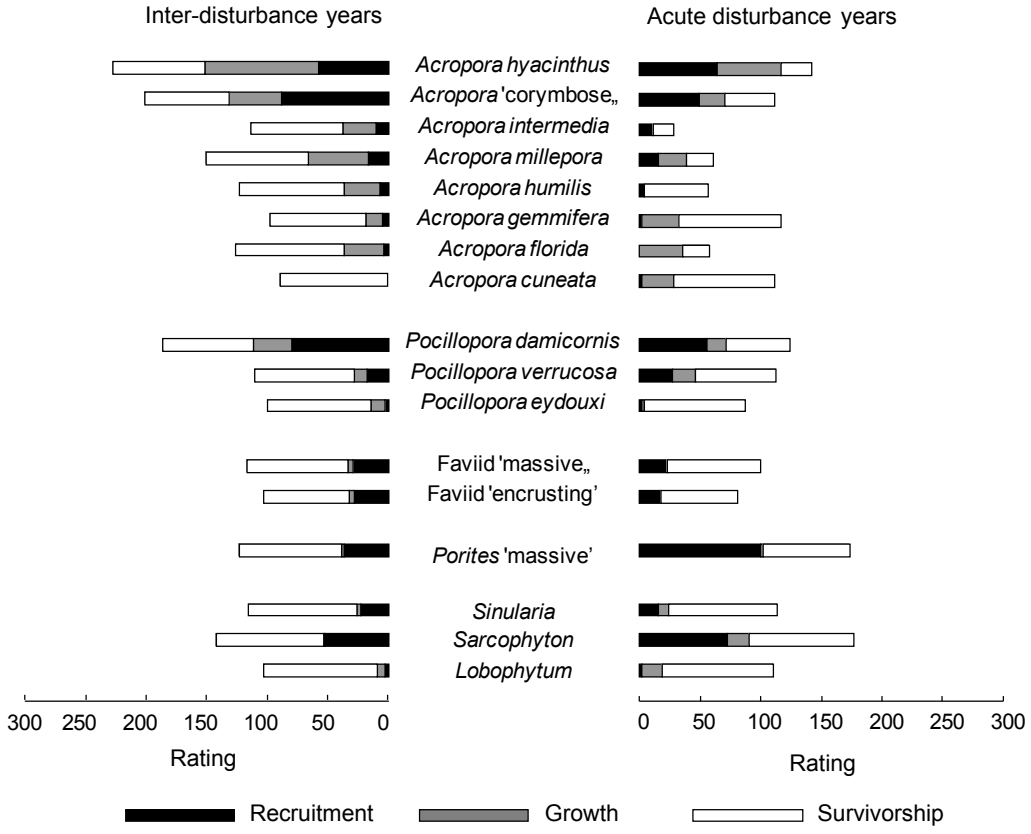


Fig. 2.6 Performance ratings for physiognomic groups in "Acute disturbance" and "Inter-disturbance" years. Recruitment, growth and survivorship rates for each physiognomic group are presented on a scale of 0-300.

Tuning the model

The best-fit model trajectory for total hard coral cover was obtained using variable growth throughout, and zero background mortality for all except the last inter-disturbance period, 1997-2003 (Fig. 2.7, Table 2.2a), when hard coral failed to recover. For soft corals, selecting between these options had little effect. The effect of changed interaction and recruitment scenarios (below) were run using the best-fit model parameters, i.e. variable growth and background mortality included for the last inter-disturbance period.

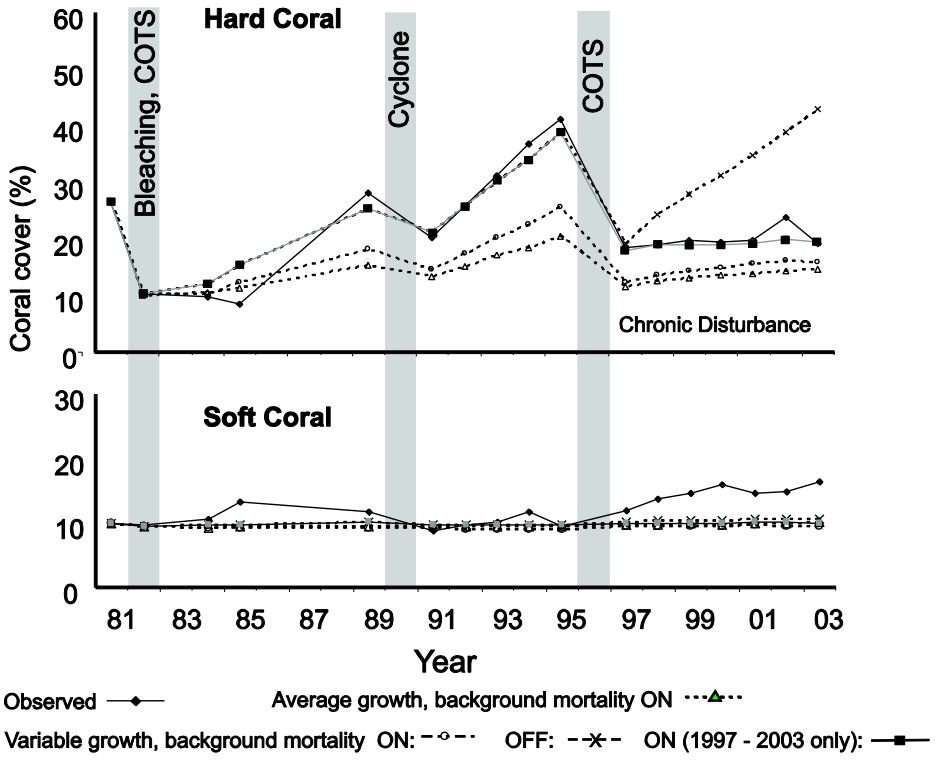


Fig. 2.7 Percentage cover of hard and soft corals through time. Comparison of Observed and Model trajectories.

Effects of interaction and recruitment

The model trajectory based on interaction outcomes measured from the photographs produced a better trajectory than the three models given arbitrary interaction outcomes (Fig. 2.8a, Table 2.2b). However all model trajectories were similar irrespective of the underlying differences in the models that generated them, and all were significantly correlated ($P < 0.0001$) with the

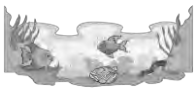


Table 2.2 Results of the Procrustes Rotation Analyses and ProTest Permutation Test on the Non-metric Multidimensional Scaling (NMDS) - Observed versus Model trajectories.

	Procrustes sum of squares	ProTest correlation	ProTest significance
a) Model selection			
Observed trajectory versus:			
Average growth, background mortality ON	0.06884	0.8054	0.0001
Variable growth, background mortality ON	0.06527	0.8167	0.0001
Variable growth, background mortality OFF	0.07097	0.7987	0.0001
Variable growth, background mortality on 1997-2003	0.03731	0.8998	0.0001
b) Interaction			
Observed trajectory versus:			
Model [Best fit model selected from (a) above]	0.03731	0.8998	0.0001
Standoff (outcomes as 0:0:100%)	0.04739	0.8707	0.0001
Equal (outcomes as 33:33:34%)	0.04769	0.8698	0.0001
Random (randomly determined probabilities of win and loss, with no standoffs allowed)	0.04698	0.8719	0.0001
c) Recruitment			
Observed trajectory versus:			
Model [Best fit model selected from (a) above]	0.03731	0.8998	0.0001
Failed Recruitment	0.04857	0.8673	0.0001
Mean recruitment rate across all physiognomic groups	0.04336	0.8825	0.0001
Double the mean recruitment rate of each physiognomic group	0.05379	0.8518	0.0001
Ten-fold the recruitment rate of each physiognomic group	0.05029	0.8622	0.0001
d) 100 year models			
Observed trajectory versus:			
Model [Best fit model selected from (a) above]	0.01006	0.8798	0.050205
Disturbance every 16 years	0.0252	0.6587	0.18162
Disturbance every 8 years	0.0201	0.7406	0.083108
Disturbance every 6 years	0.02137	0.7211	0.12241
Disturbance every 4 years	0.02394	0.6798	0.21732
Disturbance every 2 years	0.02578	0.6486	0.35664

ProTest correlation indicates least squares correlation between observed trajectory and the indicated model set-up (left column). Value of ProTest significance is interpreted in the same way as other statistical „p' values.

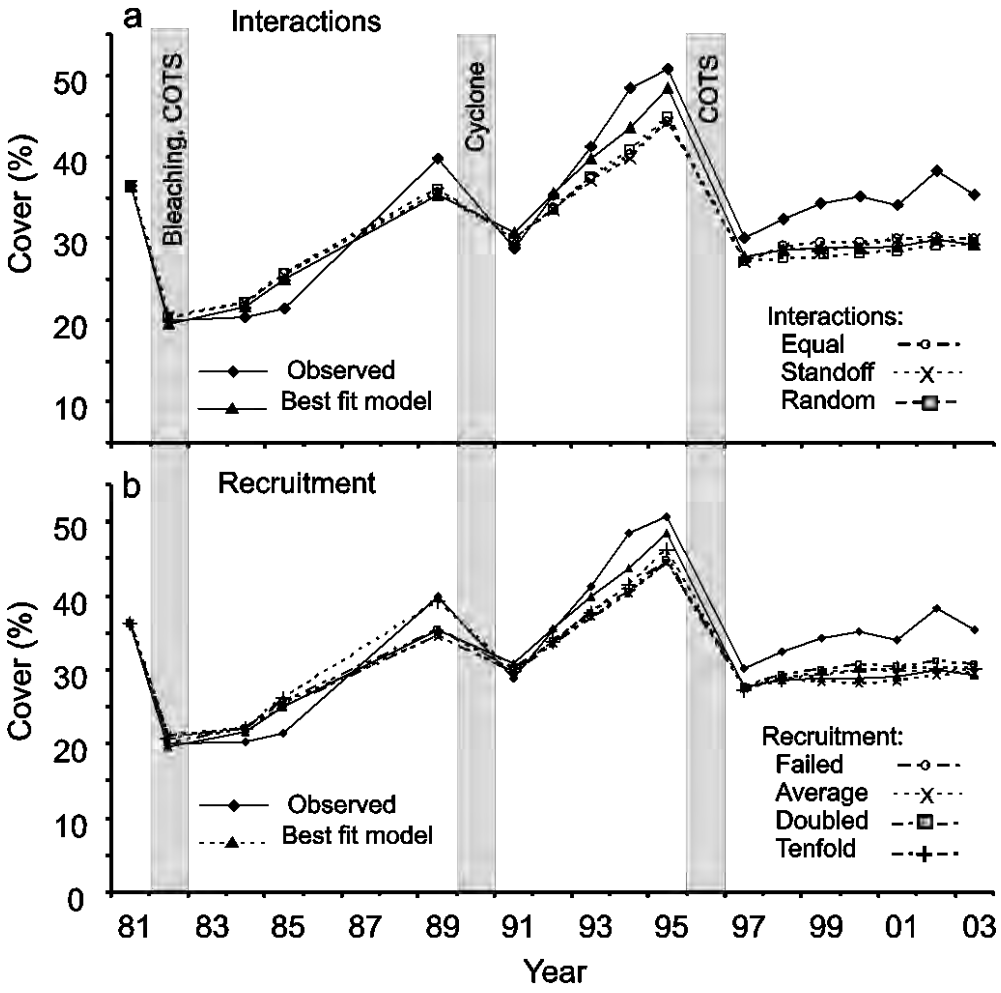
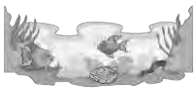


Fig. 2.8 Percentage cover of hard corals through time. Comparisons of Observed and Modelled trajectories. **a** Effects of the outcomes of interactions. **b** Effects of changed patters in recruitment.

‗observed' trajectory. Surprisingly, large differences in rates of recruitment did not significantly influence the model trajectory, even when recruitment was increased ten-fold across all physiognomic groups (Fig. 2.8b, Table 2.2c).

Predictions from 100 year models for changed disturbance frequency

An 8 year disturbance frequency produced community configurations that (in the years just prior to a disturbance) were closest to the least ―disturbed" observed communities (Fig. 2.9a; p = 0.083108, Table 2.2d), i.e. dominated by *A. hyacinthus* with contributions from *P. damicornis* and *Acropora* ‗corymbose'. However even these diverged markedly from the observed community after about 20-30 years (Fig. 2.9a, d), when physiognomic groups were successively



lost as both total coral cover and the monopolization by *A. hyacinthus* increased. This divergence started sooner with a 16 year disturbance frequency (Fig. 2.9c), in which *A. hyacinthus* reached almost 100% cover after 96 years (Fig. 2.9a) and only four of the original 17 groups survived. At the other end of the scale, the 2 year disturbance frequency no longer supported a hard coral-dominated community after 100 years: most of the low total coral cover (Fig. 2.9g) comprised soft corals (3 genera; Fig. 2.9a). Four and six year intervals (Fig. 2.9f, e) allowed total coral cover to grow with relatively small declines in richness.

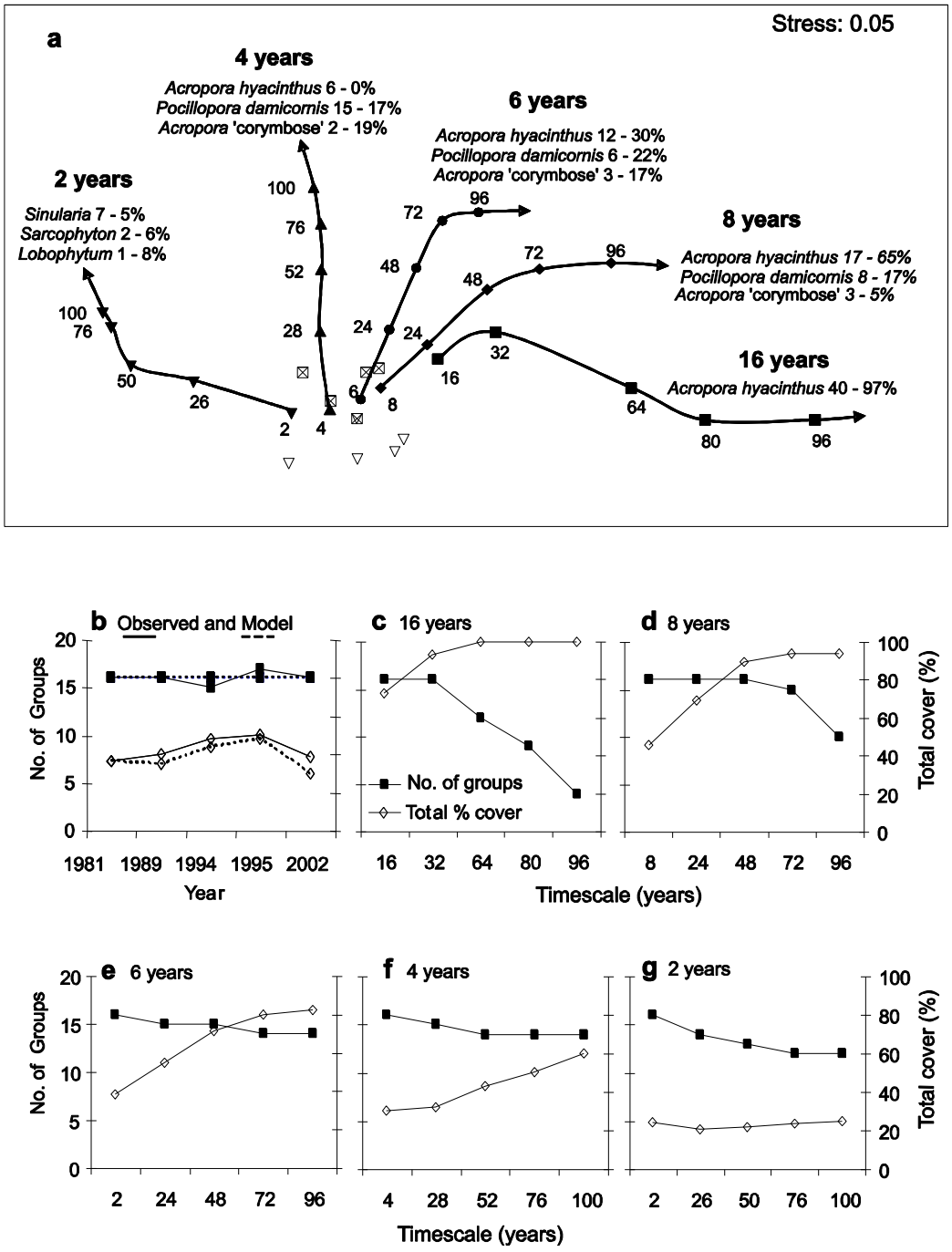
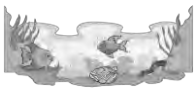


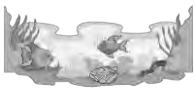
Fig. 2.9 Predictions from 100 year models for changed disturbance frequency. **a** NMDS of physiognomic composition and abundance on years preceding disturbances. Disturbance intervals were 2, 4, 6, 8 and 16 years (with numbers along each trajectory indicating year the community data was extracted). The dominant physiognomic groups for each disturbance frequency are listed as a range indicating community composition for the first and last community respectively, i.e. with an 8 year disturbance frequency, there was 17% *Acropora hyacinthus*, 8% *Pocillopora damicornis* and 3% *Acropora* „corymbose', whereas after 96 years they were at 65%, 17% and 5% respectively. The least disturbed communities from 1981-2003 (Jan 1981, 1989, 1994, 1995, 2002) are represented from the Observed and Model communities. **b–g** Summary of the number of Physiognomic groups and Total percent cover for each disturbance frequency.



Discussion

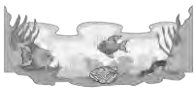
Crown-of-thorns starfish, coral bleaching and cyclones are large scale disturbances that can exert considerable impact on mid-shelf reefs of the northern and central Great Barrier Reef (Endean and Cameron 1990; van Woesik et al. 1991; Done 1992; Berkelmans et al. 2004). In this study the key parameters driving a local reef community were measured and it was possible to approximately replicate the dynamics of this community using the individual-based model Compete©. Various methods were investigated to construct a model that was reasonably faithful in its representation of the community over the 23 year study period. A model based on variable growth rates performed better (closer match to observed) than one based on fixed average growth rates. This allows both exceptional years and size-dependent growth rates to affect community trajectory in a way average growth alone cannot (c.f. Done et al. 2007).

Up until 1996, the 23 year model would only satisfactorily reproduce the community trajectory if all modelled mortality was confined to acute disturbance years only. Beyond that date (1997-2003) it was necessary to introduce background mortality into the model to adequately replicate the lack of post-1996 recovery of hard corals. Up until 1996, the study site had been characterised by inter-disturbance periods in which hard coral cover either regained or exceeded previous levels and there was low mortality. It is proposed that this community has entered a new phase in which inter-disturbance ‗recovery' periods are characterised by chronic disturbance – the model's ‗background mortality' – caused by predation, bleaching and disease. The study community was still recovering from the major 1996 crown-of-thorns starfish outbreak when region-wide mass bleaching occurred in 1998 and 2002 (Berkelmans et al. 2004), and there were also small numbers of crown-of-thorns starfish in and near the site at those times (Sweatman et al. 1998; Pratchett 2005; personal observations). Although a number of corals at the site partially bleached during both bleaching events there was not a marked increase in coral mortality (i.e. complete colony death). However bleaching can reduce coral growth rates, lower fecundity and increase the incidence of disease (Baird and Marshall 2002; Harvell et al 2002; Douglas 2003), all of which could slow recovery. It is proposed that since 1996 there has not been a typical inter-disturbance period free of disturbance in which coral can fully recover. Instead, various



disturbances including residual crown-of-thorns starfish, low-level bleaching and secondary disease, have impacted the community and kept coral cover stable at low post 1996 disturbance levels.

Neither recruitment rate or interaction outcome had much impact on the model trajectory. Failed recruitment did not cause a significant drop in coral cover and alternately a 10-fold increase in recruitment did not cause a significant rise. The lack of sensitivity to this order of magnitude variability in recruitment reflects very low absolute densities of recruits recorded at the site. (The combined average totalled across all groups was only 27 recruits per year, which, based on a size of 25 x 25 mm per model recruit, would cover about 0.05% of the whole area). Moreover, the 7-8 year interval of recruit growth between disturbances would not be sufficient time for such a low starting percentage - even multiplied ten times - to make a significant contribution to cover compared to the growth of large established colonies. Estimates of recruitment at the site may have been low, due to the overtopping growth of *A. hyacinthus*. It cannot be assumed that this site is generally representative of this habitat at large in respect of recruitment rates, but this study does show that recruitment cannot be taken for granted as a major driver of observed changes; it can take a distant third place to survival and growth of established colonies. For interactions, the conventional wisdom is that they play a major role in shaping coral community structure and dynamics (Lang 1973; but c.f. Bradbury and Young 1983). The present study, however, indicated that interactions at this site were unimportant because frequent disturbances created a surfeit of free space and a very low incidence of competitive interaction before the next disturbance arrived. Average space at the site that was unoccupied by any of the physiognomic groups was about 68% and maximum coral cover was 40%. In other habitats with comparable colony sizes and low total coral cover, interactions among established corals and other macro-benthos may similarly be of minor importance, and their influence also approximated by arbitrary models. In summary, the model suggests that recruitment and interaction play a minor role in structuring this community over the 2-decade timescale of observations, and that the major drivers of community are time since disturbance and growth.



There is widespread concern that global change is degrading the fundamental structure, function and provision of services by ecosystems of all kinds. For coral reefs, numerous studies have shown that their degradation is often manifest as a persistent phase shift to non-reef-building forms such as macro-algae, soft corals or to overgrazed barrens (Done 1992; Hughes 1994; Wooldridge et al. 2005). There was no such tendency observed in the site in the period 1981 to 2003. However the need to introduce background mortality to accurately model from 1997-2003 suggests that a period of changed disturbance regime and community dynamics may have already commenced.

The model was therefore used to assess community persistence and resilience under a range of different disturbance frequencies. The model in which a major disturbance event arises every 16 years (which is about twice as long as the average observed interval) produced a community that after 100 years became dominated by the hard coral *A. hyacinthus* (97%). Although the maximum cover of *A. hyacinthus* at this site has only been recorded at 17%, a cover of 75% and more is not uncommon in similar habitats on the GBR (personal observations of the authors). Disturbance every 2 years led to a community that no longer supported hard coral and only low levels of soft coral persisted. There are places where soft corals do monopolize large areas (Dinesen 1983; Fabricius 1997; Ninio et al. 2000) and it is plausible that soft corals could expand in the site, especially under increased disturbance frequency and background mortality levels that limit hard coral recovery. A disturbance interval of eight years with current rates of recruitment, growth and mortality most closely reproduced the mixed hard coral dominance observed at the site in the 1980s and 90s (but only for the first 20-30 years of the 100 year projection). These 100 year projections did not include the chronic background mortality that this study suggests has retarded hard coral growth since 1996. This raises the question as to whether a community suffering chronic background mortality will be able to recover its former abundance, species composition and size class following acute disturbances, or indeed, decline even further.

CHAPTER 3

DECADAL TRAJECTORIES OF TWO SHALLOW CORAL ASSEMBLAGES: EFFECTS OF COMPOSITION, DEPTH, SHELTER AND INITIAL STATE

Research for this chapter has been prepared for submission:

Wakeford M, Done TJ, Johnson CR. Decadal trajectories of two shallow coral assemblages: effects of composition, depth, shelter and initial state. *Coral Reefs*

Contributions: Wakeford 70%; Done 20%; Johnson 10%.

Abstract

This study compares 25 year trajectories of two coral assemblages at Lizard Island, Australia, one at a sub-tidal (~2 m depth) and one at an inter-tidal site. While coral species represented at the two sites (separated by several kilometres) were similar, their starting states and 25 year trajectories describing temporal change in community structure were very different. A spatial model was parameterized to reproduce the observed changes in coral cover and composition at each site, using demographic rates and interaction outcomes measured independently at each site. The modelling suggested that differences between sites in disturbance regimes (mortality frequency and patch size) were driving community dynamics much more strongly than differences in growth, recruitment or pair-wise interaction outcomes (win, loss or stand-off). In addition, there was an apparent qualitative switch from acute to chronic disturbance at both sites around the turn of the century.

Introduction

Understanding the nature and causes of spatial variability in the structure and dynamics of sessile biological communities is a key aspect of ecology (e.g. Pickett and White 1985; Scheffer and Carpenter 2003), including coral reef ecology (Connell 1978; Hughes 1989; Connell et al. 1997). The concept of coral communities as interim stages on a trajectory of change, periodically set back by disturbance, is well established (Connell 1978; Pearson 1981; Sousa 1984; Done 1987; 1992; Hughes 1994; Huston 1994). In recent times the variety, extent and intensity of disturbances affecting coral reef communities has increased dramatically (Wilkinson 1999; Hughes et al. 2003). Extensive coral mortality has been caused by coral bleaching (Hoegh-Guldberg 1999; Kleypas et al. 1999), outbreaks of coral eating predators (Seymour and Bradbury 1999) and disease (Harvell et al. 2002; Rosenberg and Ben-Haim 2002; Ainsworth et al. 2007; Rosenberg et al. 2007). In addition, cyclones can severely impact localised areas of reefs (Hughes and Connell 1999; Fabricius et al. 2008) and anthropogenic disturbances such as deteriorating coastal water quality can threaten reef health (Wilkinson 1999; McCulloch et al. 2003; Fabricius 2005).

Recovery of corals following disturbance can be forestalled if a follow up disturbance occurs too soon (Done et al. 2007) or if coral recruitment fails. In the longer term a change in the disturbance regime might be manifest as the introduction of new kinds of disturbances, shifts in the frequency or intensity of disturbances, or by synergistic effects among multiple disturbances and stressors. If a community suffers an increase in disturbance frequency that shortens recovery period, then the intensity of subsequent disturbances may be masked or difficult to detect, especially if the most susceptible component of the community has already been removed. The impact of disturbance may shift from acute pulse events to a chronic regime. One example is the retention of small numbers of crown-of-thorns starfish, *Acanthaster planci*, in an area following an outbreak. Another is reduced fecundity in corals (Ward et al. 2002) or increased susceptibility to disease (Richmond 1993; Peters 1997) caused by sub-lethal bleaching events (McClanahan et al. 2009).

Whilst shifts in disturbance regimes may have considerable long-term consequences for community structure and dynamics, they can be difficult to detect. Similarly, it can be very difficult to detect a shift from the „normal' dynamics and fluctuations of a healthy and properly functioning reef or reef system to a new and fundamentally different kind of dynamic that may represent, for example, long term loss of resilience. Long-term ecological datasets are fundamentally important resources for examining processes that support or undermine ecosystem resilience, i.e. the ability of reefs to absorb disturbance, resist phase shifts, reorganise and adapt to change (Holling 1973; Gunderson 2000; Nyström et al. 2000; Bellwood et al. 2004). There are few historical baselines by which to judge and assess recovery (Connell 1997) and this is particularly true for „pristine" coral reefs; for example, the first systematic surveys of the Great Barrier Reef (GBR) began in the late 1960s after a severe outbreak of the crown-of-thorns starfish had devastated coral populations (Knowlton and Jackson 2008).

Local physical and biological features can affect the response of a coral community to a given disturbance. A site's degree of exposure to waves and air; its depth, and topography; and the acclimatization of its biota to local conditions can all influence susceptibility to particular disturbance events (Brown et al. 2000; Fitt et al. 2001; Done 2003; Pratchett 2005; Madin et al. 2006).

This study investigates changes in coral community dynamics at two sites at Lizard Island (I South Reef and II North Reef) subject to a series of disturbances over a 25 year period (1981-2005). The aims of the study were to 1) compare community trajectories at the two sites; 2) look for evidence at North Reef of a qualitative shift in disturbance regime similar to that reported for South Reef (formerly called Lizard 1, see Chapter 2); and 3) gain insights into the underlying community dynamics including differences between the sites using of a spatial model parameterized by disturbance schedules and ecological parameters.

As for South Reef, the approach at North Reef was to parameterize the model based on field observations to obtain the best fit between the predicted and observed trajectories of the 25 year study period. Particular attention is given to identifying time periods where parameters need to

be altered to achieve a reasonable fit between predicted and actual trajectories. This is an heuristic approach in which the parameterization and differences between sites inform the development of a conceptual model to identify both the contrasting drivers of change at the two sites and similarities in gross dynamics. These considerations help to identify processes manifest at different scales that drive the dynamics of reef sites in general.

Materials and methods

Study sites

These two sites are several kilometres apart on opposite sides of Lizard Island (Fig. 3.1) and were established with slightly different plot layouts. South Reef (an 8 x 4 m plot; Figs. 3.2a, 3.3a) lies ~ 1.5 m below extreme low tide and North Reef (a 10 x 3 m plot; Figs. 3.2b, 3.3b) emerges at extreme low tides. South Reef is directly exposed to strong swells from the south-east for much of the year. Waves surge across the site and periodically dislodge corals (Madin et al. 2006) but do not break directly on the corals. North Reef is exposed to direct wave impact from the north-east and north-west (mainly in summer months), and to refracted waves during south-easterlies. Waves plunge onto and break directly onto corals at extreme low tides. At the beginning of the study in 1981, South Reef had a 20% cover of an *Acropora*, *Pocillopora* (Scleractinia) and *Sarcophyton* (Alcyonacea) dominated assemblage (Fig. 3.3a), while North Reef had an 80% cover of an assemblage strongly dominated by robust plate *Acropora* (see below).

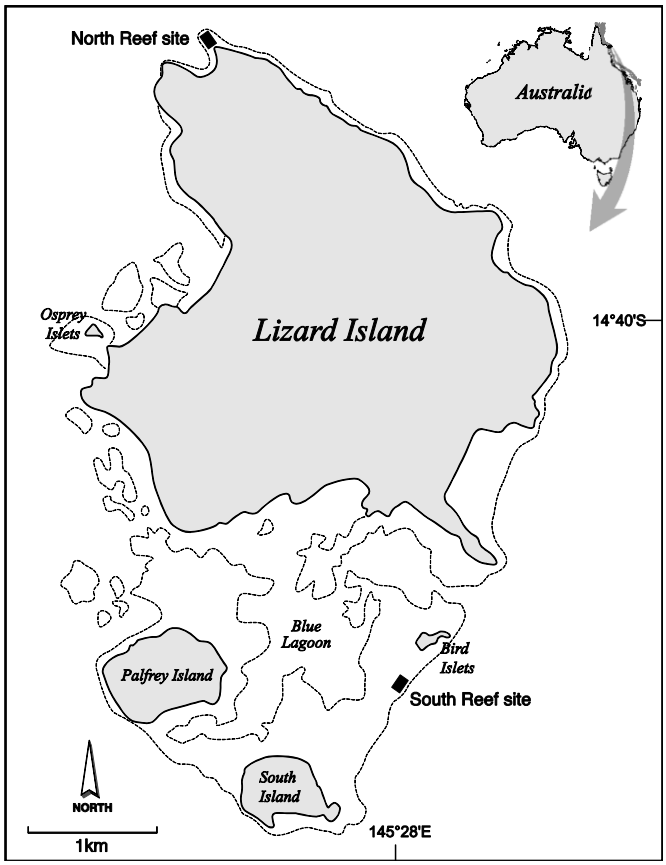
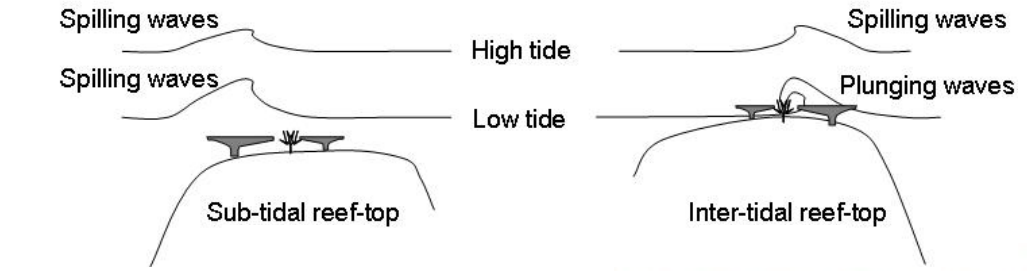


Fig: 3.1 Location map of Lizard Island and the two study sites.

Sampling

The study sites are permanently marked plots on the reef that were monitored most years using near-vertical stereo photography (Done 1981). In some years inclement weather prevented site photography and monitoring was temporarily suspended from 1986-1988. From 1981 – 2005, photographs were taken in 18 of the 25 years for South Reef (Fig. 3.2a), and 20 of 25 years for North Reef (Fig. 3.2b). Photographs were taken ~ 2 m above the substratum at 1 m intervals along tape measures stretched between permanent steel pegs driven into the reef.

Point sampling of the stereo images was used to map and quantify temporal change in percentage cover of sessile benthic organisms. For 1981, an initial stylized map was produced



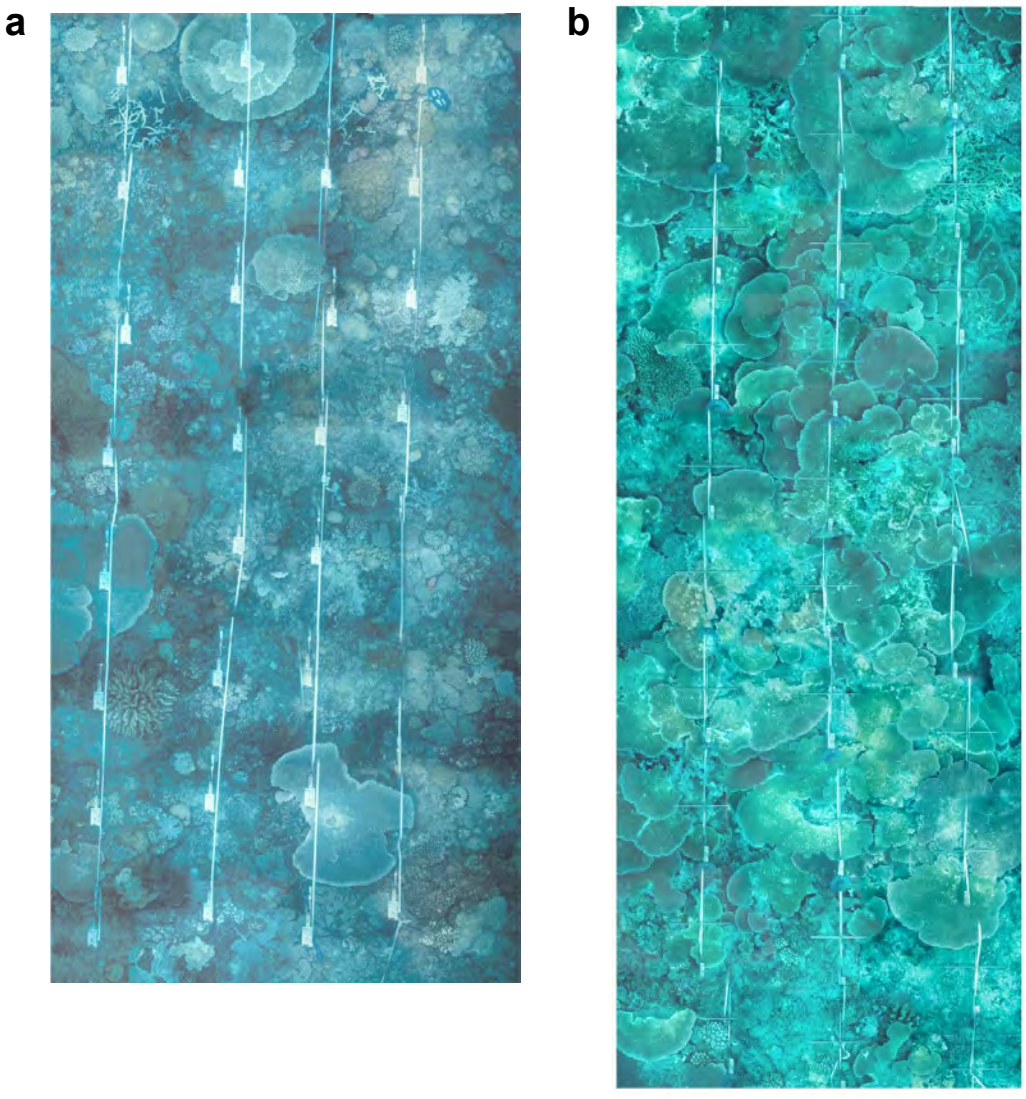


Fig.3.2 Topography and photo mosaic of study sites. **a** South Reef in 1981, approximate area 4 m x 8 m comprised of 32 photographs. **b** North Reef in 1984, approximate area 3 m x 10 m comprised of 30 photographs.

by recording the benthos underlying a 10 x 10 grid of evenly spaced points for each photographic pair, identified to the highest possible taxonomic level (usually genus or species). Each coral or substratum type beneath a grid point was assigned to one of the17 physiognomic groups. The community maps produced for 1981 provided the starting maps used in a spatial model (see below), in which it was assumed that the observed benthic attribute at each point fully occupied a 100 x 100 mm square of the base map. After 1981, the percentage cover of these groups on each sampling occasion was estimated using100 (South Reef), or 10 (North Reef) evenly spaced points per photograph (the lower number of points was found to be more than adequate for plot-wide estimates of coral cover and composition). The maximum diameter of all colonies of the dominant cover in both sites (plating *Acropora* colonies) was estimated from the digitised images using the tape measure for scale. Through the time series, these measurements provided a record of contributions of growth and recruitment of *Acropora* plates to coral cover.

The model Compete© (available at http://www.zoo.utas.edu.au/CJPblist/Compete%20program/), uses cells on a landscape to represent the spatial arrangement of colonies competing for space. The user-defined initial landscape (the starting base map, see above) represents the community at time zero and cells get synchronously updated based on rates of growth, mortality, recruitment, and interaction outcomes measured at the sites. A sub-set of the photographs (the same 14 or 12 pairs on each trip for South Reef and North Reef respectively, see Fig. 3.3) from areas of the site supporting a range of corals species was selected to maximise the number of demographic measures obtained. Stereoscopic observation and image measurement were used to quantify rates of growth, mortality and recruitment, and the outcomes of inter-specific interactions at each site, for each of 17 physiognomic groups, identified mainly to genus (Table 3.1). The 25 y study was divided into ‗inter-disturbance periods' and ‗disturbance periods', based on the observed trajectories of total hard coral cover (see Results). Rates of growth, mortality and recruitment were determined separately for each period and site. *Growth rate* for each physiognomic group was the annual change in colony area converted to a rate of linear extension. *Mortality rate* was the mean number of whole colonies of each physiognomic group in the sub-sample dying in a

year. *Recruitment rate* was the number of new colonies appearing in the sub-sample divided by the number of years since the last observation. The *outcome of interactions* (pooled over all periods at each site to provide adequate sample size) between every possible pair of physiognomic groups was based on enumeration of wins, losses or stand-offs, converted to a probability. Thus, two different methods were used to quantify changes in space occupied by different physiognomic groups, the former essentially directly observing changes (through point sampling) and the latter using demographics events and the model in Compete© to infer changes.

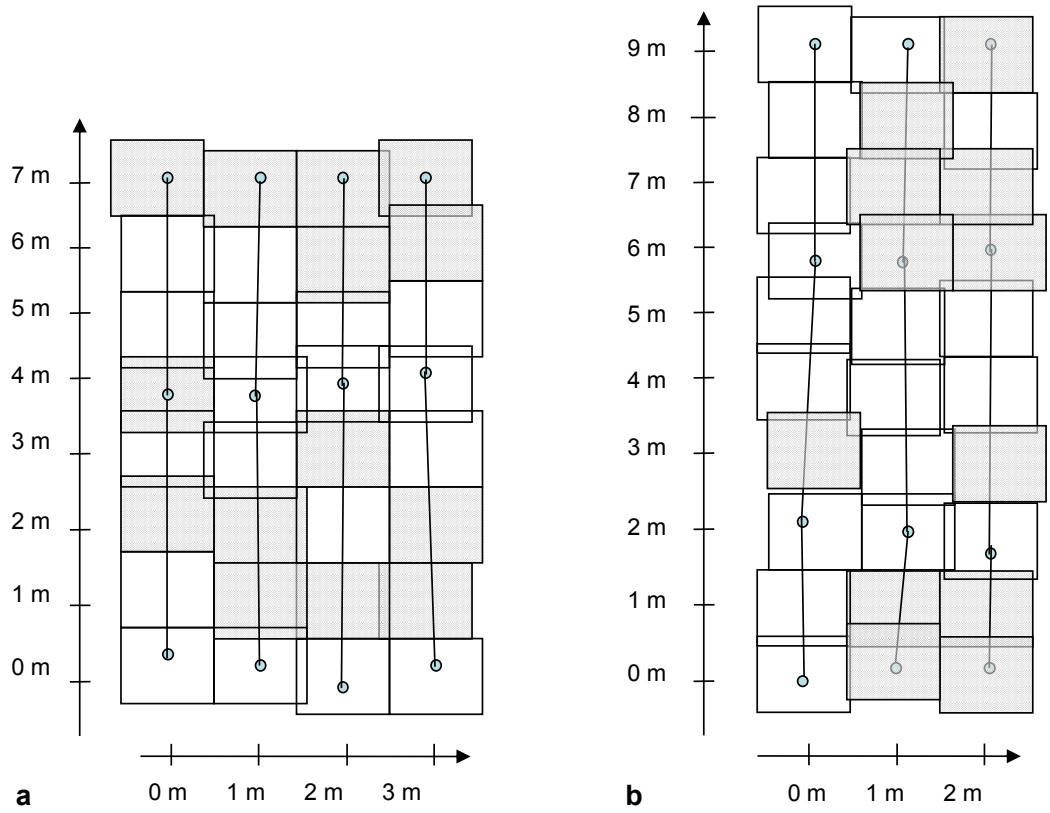


Fig. 3.3 Detail of study sites. Rectangles are areas covered by the digitised 35mm slides. Dots represent steel pegs driven into the reef and lines connecting them represent the tape measures laid during photography. Shaded rectangle **a** South Reef (14), and **b** North Reef (12), represent the subset of photographs analysed to derive data for rates of mortality, growth, recruitment and interaction outcomes.

Table 3.1 The 17 physiognomic groups at South Reef and North Reef showing percent cover for the period 1981-2005.

	South Reef				North Reef			
Pysiognomic group by family	**Average % cover**	**Min**	**Max**	**S.E.**	**Average % cover**	**Min**	**Max**	**S.E.**
Acroporidae								
Acropora „plates'	5.0	0	16.9	1.5	30.3	9.7	73.4	5.0
Acropora „croymbose'	3.4	0.2	7.7	0.6	2.5	0	6.4	0.5
Acropora intermedia	1.5	0	4.4	0.4	1.3	0	4.8	0.2
Acropora millepora	0.5	0	1.1	0.1	1.7	0	4.8	0.3
Acropora humilis	0.4	0	1.1	0.1	0.2	0	1.0	0.1
Acropora gemmifera	0.4	0	0.8	0.1				
Acropora cuneata	0.2	0	0.8	0.1				
Acropora florida	0.2	0	0.6	0.1	0.7	0	1.8	0.1
Pocilloporidae								
Pocillopora damicornis	5.3	3.2	6.9	0.3	0.3	0	1.2	0.1
Pocillopora verrucose	1.5	0.8	2.4	0.1	0.5	0	1.5	0.1
Pocillopora eydouxi	0.2	0	1.0	0.1	0.7	0	2.7	0.2
Faviidae								
faviid „massive'	1.8	0.9	3.1	0.2				
faviid „encrusting'	0.2	0	0.4	0.0				
Poritidae								
Porites „massive'	1.7	1.0	2.5	0.1	0.4	0	1.8	0.1
Alcyonidae (Soft corals)								
Sinularia spp.	6.9	4.0	9.1	0.4				
Sarcophyton spp.	3.8	1.9	6.1	0.3				
Lobophytum spp.	1.5	0.6	3.6	0.3				

Comparing the Compete© model outputs to observed changes of community cover measured through point sampling provides a check on whether the way that growth, mortality, recruitment and competition is characterised in Compete© is a reasonable approximation of how these processes influence coral cover.

Comparing ecological parameters between sites

T-tests were used to test for differences between sites and time intervals in mortality, growth, and recruitment. Two tailed, unpaired t-tests compared 12 years of inter-disturbance measures from South Reef, to 8 years of measures from North Reef. The t-tests compared between sites and for each physiognomic group 1) the annual growth rate of individual colonies; 2) the total number of colonies dying per unit area per year; and 3) the number of new colonies per unit area per year. T-tests were carried out using GraphPad Software Inc. (1999-2005).

Fisher's Exact Test (Kirkman 1996) was used to compare between-site differences in interaction outcomes for paired physiognomic groups (Win : Loss : Standoff). Where the observations for a paired physiognomic group were less than eight at either site, sample size was considered too small, and a comparison was not made. Eight pair-wise combinations among the 10 groups were tested (out of 45 possible combinations). The null hypothesis was that site location did not affect outcomes of interactions.

Modelling community trajectories

Trajectories of cover of each physiognomic group were modelled separately for each site and period (disturbance versus inter-disturbance periods) using the Compete© model. Rates for growth, mortality and recruitment were specific to both period and site, whereas probabilities of interaction outcomes were averaged over the entire study period for each site (to provide adequate sample size). The disturbance schedule for each site was modelled based on observed mortality rates during disturbance periods. During inter-disturbance periods, mortality rates (which measure total colony mortality only) were set to zero, as partial mortality incorporated into growth measures, adequately modelled the low _background mortality' during these periods (see Wakeford et al. 2008). Overall, an heuristic approach was adopted, based on manipulation of demographic model inputs to obtain a close fit to the observed trajectory. Simulations were run over the 25 y study period 1981 - 2005, with each time step representing one month. Compete© uses a probabilistic (stochastic) cellular automaton as its kernel, with mortality, growth

and recruitment expressed as conditional probabilities of cell occupancy at each time step. The models of both sites were parameterised from the observations described above and following the methods outlined in detail in Wakeford et al. (2008). *Recruitment* was ~~"o~~pen" and thus independent of the relative abundance of physiognomic groups on the current landscape. In recruiting to an ~~"e~~mpty" cell, an individual coral was selected at random from any physiognomic group that had existed in the system, and would recruit to the empty cell with a monthly probability P = R/12, where R is that group's average number of recruits per year (N = 25 y). *Growth rate* was converted to a monthly probability of growth into an empty cell. Note that this was net growth of colonies in a time period and included both positive and negative changes in colony area, i.e. it incorporates *partial mortality* for each time period. *Mortality rate* was converted to a probability of mortality of an average sized colony for each group. Due to limitations of the model, only a single mortality patch size was specifiable for all groups. The size chosen was the average size of *Acropora* plate colonies that died during a particular period. To compensate for differences in actual colony sizes of the different groups, their individual probability of dying was adjusted in accordance to the ratio of their average size compared to the average size of dying *Acropora* plates, e.g. probability was doubled for groups with average size double the average size of dying *Acropora* plates. The *outcome of interaction*s between every possible pair of physiognomic groups was based on observations at each site and converted to a probability of win, loss or stand-off. In the model, if a ~~"c~~entral" cell was occupied by physiognomic group Y, then a neighbouring cell X was chosen at random, and X overgrows Y with probability *Pr*XY**G*XY where *Pr*XY was the probability of X winning an encounter with Y, and *G*XY is the growth rate of X over Y.

In summary, the model was used in this study to determine whether (1) local ecological process measured at North Reef could be modelled to produce a community trajectory similar to the observed community over 25 years; (2) whether there is any evidence of a qualitative shift in community dynamics at North Reef similar to that already reported for South Reef (i.e. a change in background mortality evidenced by having to include mortality during the last inter-disturbance period); and (3) whether good predictions for the North Reef community could be

modelled using South Reef parameters for growth, recruitment and interaction outcomes coupled with the North Reef disturbance schedule. This was done with the view to determining which parameters were most important in driving community dynamics.

Results

Observed community dynamics at the study sites

South Reef

The South Reef community supported 17 physiognomic groups in total and was characterised by relatively high abundances of 3-4 groups over the study period (Fig. 3.4a). Of the 17 physiognomic groups, 14 were hard corals and three were soft corals from the family Alcyoniidae (Table 3.1). Total cover of hard corals was ~26% when the site was first surveyed in 1981, and peaked at 41% cover in 1995. *Pocillopora damicornis, Acropora* plates and ‗corymbose' *Acropora* were the most abundant hard corals. *P. damicornis* had fairly constant cover over the study period, whereas *Acropora* plates had high mortality during disturbance events and grew quickly to dominate cover during inter-disturbance periods. Hard coral cover, particularly that of *Acropora* plates, fell steeply in 1982 and 1990, but subsequently either regained (post-1982) or exceeded (post-1990) previous levels. In contrast, following disturbance decline in 1996, recovery of hard coral cover was minimal due to the failure of *Acropora* plates to regain their former high levels. *Acropora* plates dropped from a high of 17% cover in 1995 to below 2% for the remainder of the study (i.e. 9 years until 2005).

North Reef

Only ten of the 17 physiognomic groups at South Reef were also present at North Reef (Table 3.1), and there were no soft corals at North Reef. In the 1980s, North Reef was much more space limited than South Reef (82% hard coral cover - dominated by *Acropora* plates (77%)). Plates

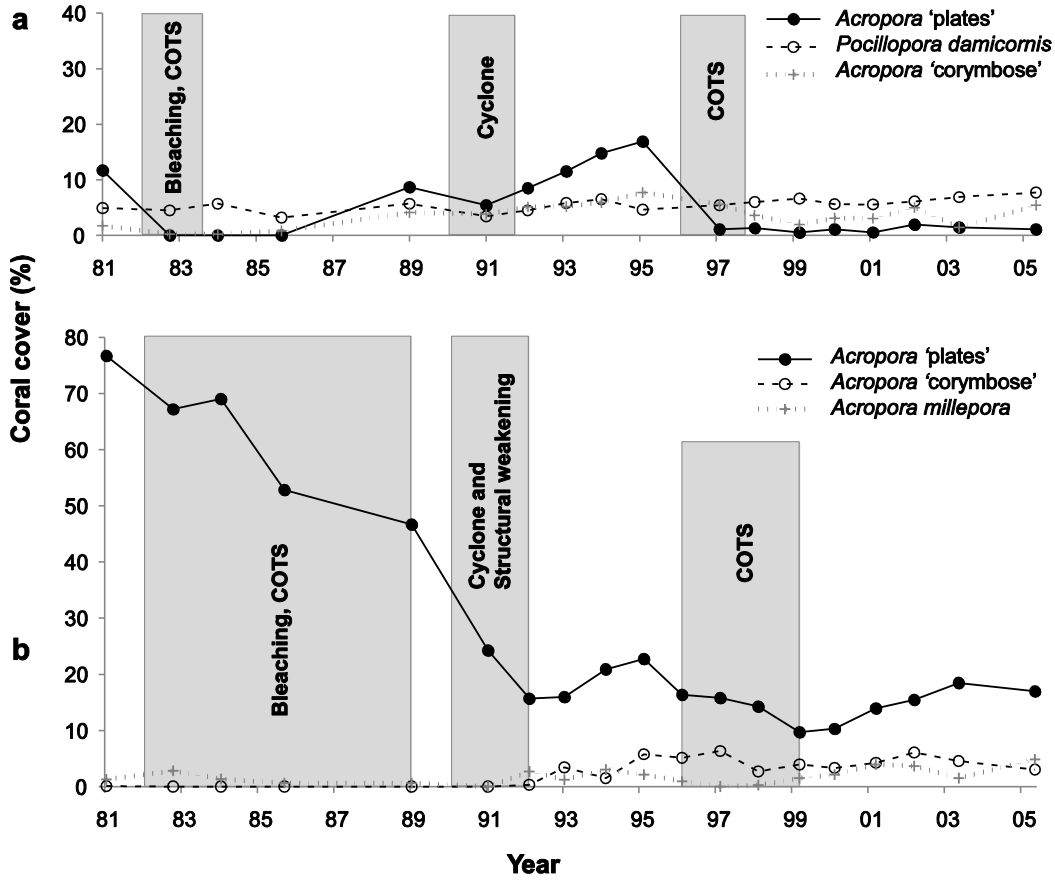


Fig. 3.4 Temporal patterns in cover of the most abundant corals at the study sites, 1981-2005. *Vertical bars* identify disturbance periods. **a** South Reef: *Acropora* plates, although susceptible to disturbance showed good recovery between disturbance periods. Post 1996, total cover of plates did not increase and remained low. **b** North Reef: the near mono-specific stand of *Acropora* plates showed long-term decline from 1981-1992 associated with the first two disturbance periods. Post 1999 cover of plates increased but did not recover to former levels. Decline in cover associated with disturbance typically spanned several years at North Reef (*c.f.* South Reef). Trajectories at the two sites were more closely aligned from 1992.

were up to 1.5 m in diameter and most of the plot comprised a continuous cover of individuals overlapping and/or fused together (Fig. 3.3b). Coral cover at North Reef was characterised by a steady decline over 11 years (1981-1992) in which plating *Acropora* cover fell from 77% to 16% (Fig. 3.4b). From this time onwards plating *Acropora* cover remained relatively low, although there was a short period (1993 – 1995) in which they did increase to 23% cover before a second decline to 10% cover (1996 -1999) associated with crown-of-thorn starfish (Sweatman et al. 1998; Pratchett 2005). This decline was followed by a gradual increase to 17% cover by 2005.

The photographs of North Reef from 1982 to 1984 reveal very little mortality associated with the 1982 bleaching, but distinctive patches of white skeleton and also black turf-covered areas indicated predation by crown-of-thorns starfish. By September 1985 many dead standing corals had disappeared, exposing large patches of substrata. Low level mortality continued, most likely reflecting sporadic feeding by crown-of-thorns starfish and by 1989 only a few of the original large *Acropora* plates remained. Most of these plates were eventually gone by 1991 probably dislodged by waves generated by Cyclone Ivor (1990). After a short period of coral increase (1993-5) there was another crown-of-thorns starfish infestation that caused coral cover to decline until 1999. From 2000 until 2005 there was a gradual increase in hard coral cover with plating *Acropora* increasing from 10% to 17%.

From 1993, there was an obvious increase in other physiognomic groups that had been uncommon (average cover 1% or less) from 1981 – 1989 when the site had been dominated by plating *Acropora* (albeit in decline). A similar trend was apparent at South Reef (Fig. 3.4a) through a period (1997-2005) in which plating *Acropora* did not recover.

Contrasting patterns of growth and decline

There were major fluctuations in coral cover at South Reef, divisible into six ~~"d~~isturbance" and ~~"in~~ter-disturbance" periods (Fig. 3.5a). Typically inter-disturbance periods were characterised by recovery in which hard coral cover either regained or exceeded previous levels. However the post-disturbance period 1997-2005 was unlike earlier inter-disturbance periods, with a much higher level of background mortality. The six periods and the putative causes of disturbance were as follows:

1982 disturbance: coral bleaching and crown-of-thorns starfish;

1983–1989 inter-disturbance;

1990 disturbance: cyclone damage;

1991–1995 inter-disturbance;

1996 disturbance: crown-of-thorns starfish;

1997–2005 chronic disturbance.

North Reef trajectory of coral cover (Fig. 5b) was quite different, divisible into 5 periods and putative disturbances as follows:

1981-1989 disturbance: coral bleaching and crown-of-thorns starfish;

1990-1992 disturbance: cyclone damage;

1993-1995 inter-disturbance;

1996-1999 disturbance: crown-of-thorns starfish;

2000-2005 inter-disturbance or chronic disturbance.

Modelling coral community trajectories

There were marked differences between North Reef and South Reef in model inputs needed to produce a close match between modelled and observed trajectories (Fig. 3.5). At South Reef, use of the *average* mortality rate for each individual disturbance period produced a reasonable match (Fig. 3.5a). At North Reef, by contrast, it was necessary to set mortality to the *maximum* rate to achieve a close fit (Fig. 3.5b). For mortality *patch* size, at South Reef, patch size averaged across the entire study produced a good fit. However, at North Reef, a much larger patch size (the average size of plating *Acropora* colonies dying during disturbance periods) was needed to reproduce the steady reduction in the average cover and size of plating *Acropora* over the observation period (see below). Even using these extreme parameter values, the North Reef model did a poor job in reproducing the trajectory in 1990–92. For that period, it was necessary to arbitrarily retain the larger mortality patch size of the previous period (i.e. 530 mm versus 380 mm) to get a reasonable match.

In general, confining mortality to disturbance years did produce reasonable matches up to 1997 (South Reef), and 2000 (North Reef). However, it was necessary to introduce annual background mortality to get reasonable matches beyond those years. In the inter-disturbance period of 2000-2005, the ~~–b~~ackground mortality OFF" model (i.e. mortality not included in the model - Fig. 3.5b) significantly over-estimated plating *Acropora* cover, whereas inclusion of background mortality gave a good fit. This had also been necessary for the 1997- 2005 period at South Reef (Fig. 3.5a) where it was proposed there had been a shift in the community to chronic disturbance

(Wakeford et al 2008). Although the trajectories of the two sites varied considerably up until 1991, the disturbance schedule and degree of mortality and recovery experienced by the respective communities became more closely aligned in the last 14 years of the study.

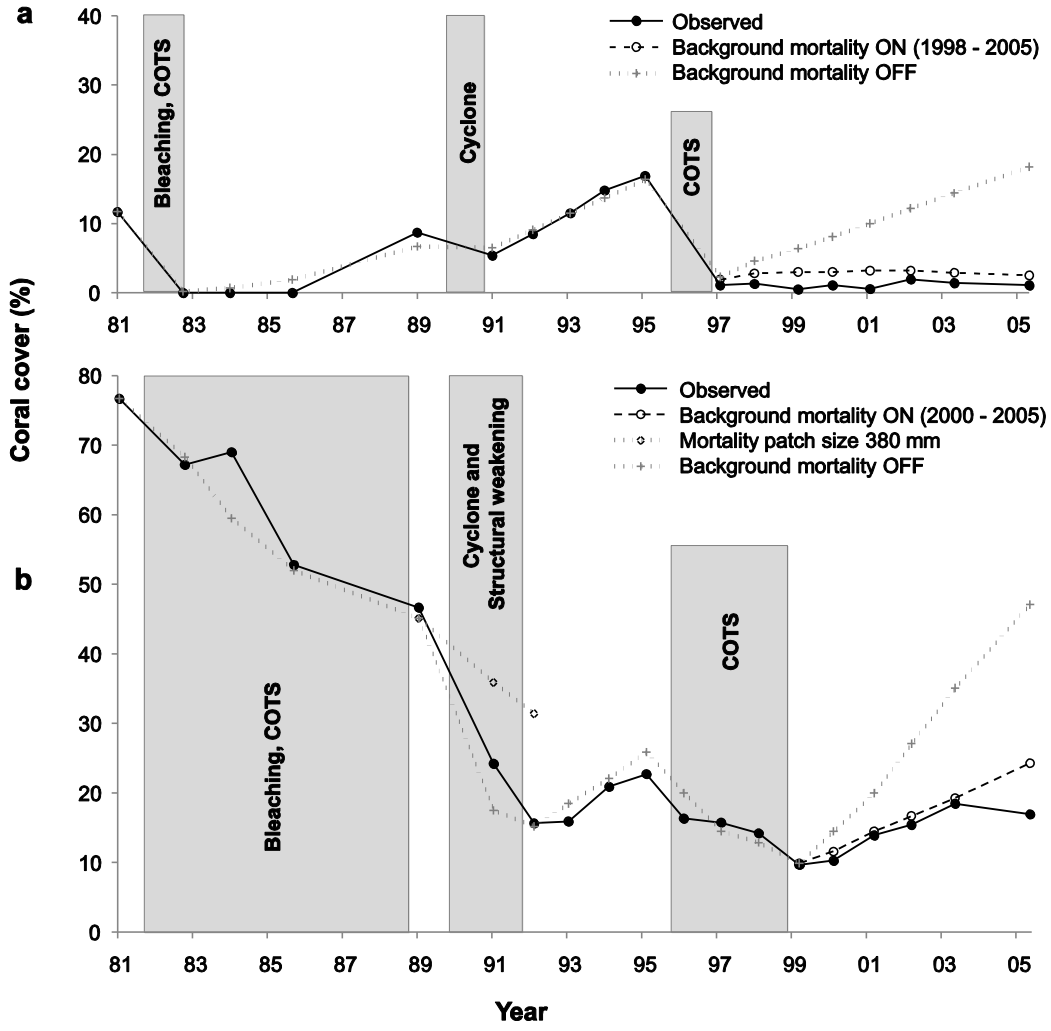


Fig. 3.5 Comparison of observed and model trajectories. *Vertical bars* identify disturbance periods. After the last disturbance it was necessary to include mortality in the model (Mortality ON 2000-2005) to simulate chronic disturbance. **a** South Reef: hard coral cover. **b** North Reef: plating *Acropora* cover. Mortality patch size set to 380 mm was inadequate to model the severe mortality in 1991-1992.

Comparison of North Reef vs. South Reef disturbance schedules and parameter rates

There were significant differences between South Reef and North Reef in demographic and interaction parameters (Table 3.2). Half of the coral groups grew faster at North Reef, plate *Acropora* recruited twice as many colonies at North Reef than South Reef, and 20% of the groups had significantly lower mortality rates at North Reef (Table 3.2; the other 80% were not significantly different). Fisher's Exact Tests comparing the outcomes of interactions between sites (averaged over the whole study) also showed significant differences in outcomes for 50% of the pair-wise physiognomic combinations (i.e. 4 out of 8, Table 3.3). Despite these differences, the model combining the North Reef disturbance schedule (mortality) with the South Reef rates for growth, recruitment and interaction outcomes (Fig. 3.6a), produced a very good fit to the observed North Reef trajectory (up until 1999) and was not much different to the trajectory produced using parameters derived entirely from North Reef (Fig. 3.5b). This indicates that differences in disturbance schedule rather than differences in growth, recruitment and interaction outcomes were more important in driving community dynamics at this site. This supports findings from the South Reef study (Wakeford et al. 2008) that recruitment and interaction outcomes play lesser roles in determining community structure. From 2000-2005 the inclusion of background morality in the model under estimates cover until 2003 but then produces a good fit up to 2005.

A qualitative change to chronic disturbance

Recruitment, growth and mortality in *Acropora* plates

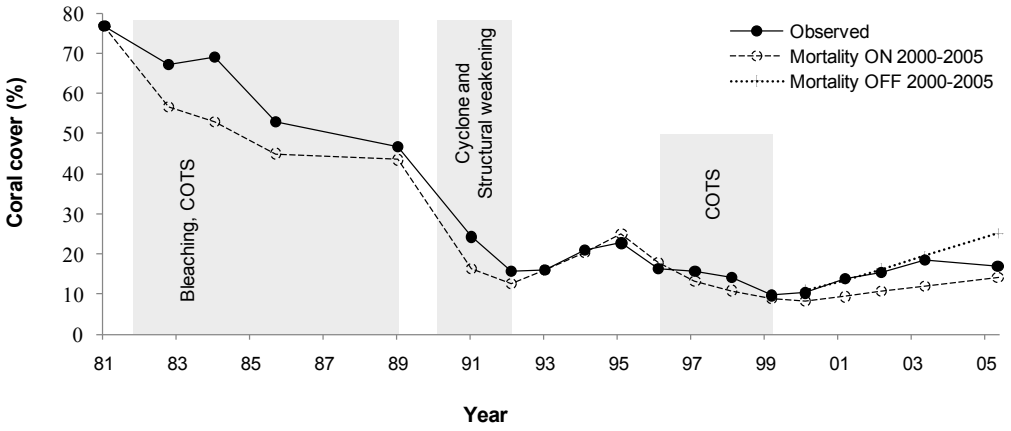
There were 1762 colonies recorded across both sites over the study period, 559 at South Reef and 1203 at North Reef. The corals were largest at both sites at the start of the study in 1981, third quartile diameters being 500 mm and 800 mm at South Reef and North Reef respectively. At South Reef (Fig. 3.7a) third quartile diameter generally decreased as cover decreased (loss of large colonies), and increased during periods of recovery such as 1989 – 1995. However from 1997 (cover of plating *Acropora* remained uniformly low (below 3%), recruitment was very low and the third quartile diameter fluctuated.

Table 3.2: Results of two tailed, unpaired t-tests comparing mean annual rate constants for growth, recruitment and mortality between South Reef and North Reef, measured during inter-disturbance periods. P-value bold when <0.05.

	Growth (mm/yr)			Recruitment (recruits/yr/m^2)			Mortality (dead colonies/yr/m^2)		
Inter-disturbance measures	South Reef mean	North Reef mean	p-value	South Reef mean	North Reef mean	p-value	South Reef mean	North Reef mean	p-value
Acropora „corymbose'	-16.709	28.849	**0.000**	0.325	0.221	0.334	0.318	**0.227**	0.434
Acropora florida	-2.587	30.539	0.262	0.018	0.000	0.226	0.011	0.011	0.996
Acropora humilis	-2.108	15.694	**0.018**	0.028	0.011	0.513	0.020	0.057	0.128
Acropora „plating'	-2.842	52.041	**0.001**	0.215	0.511	**0.016**	0.235	0.362	0.396
Acropora intermedia	-11.150	58.517	**0.000**	0.040	0.045	0.879	0.040	0.028	0.564
Acropra millepora	-1.242	12.192	0.345	0.058	0.072	0.668	0.042	0.113	0.085
Pocillopora damicornis	-17.658	20.289	0.129	0.290	0.062	**0.003**	0.285	0.060	**0.012**
Pocillopora eydouxi	-35.737	17.201	0.092	0.012	0.000	0.122	0.012	0.005	0.581
Porites 'sub-massive'	-6.432	-1.211	0.398	0.152	0.017	**0.002**	0.153	0.099	0.441
Pocillopora verrucosa	-10.701	13.202	0.**030**	0.072	0.088	0.689	0.080	0.016	**0.012**

Table 3.3 Fisher's Exact Test comparing between site differences in interaction outcome for eight paired physiognomic groups, using an exact, two sided analysis. Groups are in bold font when p-value <0.05.

Paried physiognomic groups			Win	Loss	Standoff	Two-tailed p value
		South Reef	5	0	21	
Acropora „plating'	Pocillopora damicornis	North Reef	4	0	7	0.404
		South Reef	34	3	18	
***Acropora* 'plating'**	***Acoropora* 'corymbose'**	North Reef	38	7	149	**0.000**
		South Reef	5	0	6	
***Acropora* 'plating'**	***Porites* 'sub-massive'**	North Reef	2	0	19	**0.032**
		South Reef	6	2	9	
Acropora „plating'	*Pocillopora verrucosa*	North Reef	5	0	20	0.084
		South Reef	11	0	12	
***Acropora* 'plating'**	***Acropora millepora***	North Reef	2	2	55	**0.000**
		South Reef	9	0	54	
Acoropora „corymbose'	*Porites* „sub-massive'	North Reef	0	0	21	0.104
		South Reef	3	3	26	
Acoropora „corymbose'	*Pocillopora verrucosa*	North Reef	1	0	30	0.167
		South Reef	6	2	7	
***Acoropora* 'corymbose'**	***Acropora millepora***	North Reef	3	1	50	**0.000**



	1981-89 ***Disturbance***	***1990-92*** ***Disturbance***	***1993-95*** ***Inter-disturbance***	***1996-99*** ***Disturbance***	***2000-05*** ***Chronic disturbance***
DS	North Reef 81-89	North Reef 90-92	NA	North Reef 96-99	North Reef 00-05
Growth	South Reef 82	South Reef 91	South Reef 91-95	South Reef 96	South Reef 97-03
Recruitment	South Reef 82	South Reef 91	South Reef 91-95	South Reef 96	South Reef 97-03
Interactions	South Reef interactions averaged over entire study				

Fig. 3.6 North Reef: plating *Acropora* cover. The community was modelled using South Reef growth, recruitment and interaction outcomes coupled with North Reef disturbance schedule (DS).

At North Reef (Fig. 3.7b), third quartile diameter also decreased as cover decreased (1981 – 1992). However in subsequent years, as cover increased (1993 - 1995 and 2001 - 2003) strong recruitment to the site (1994, 1995 and 2003) resulted in a reduction of third quartile diameter. There was strong recruitment of *Acropora* plates in 2003 - 2005 (Fig 3.7b) but elevated mortality after 2003.

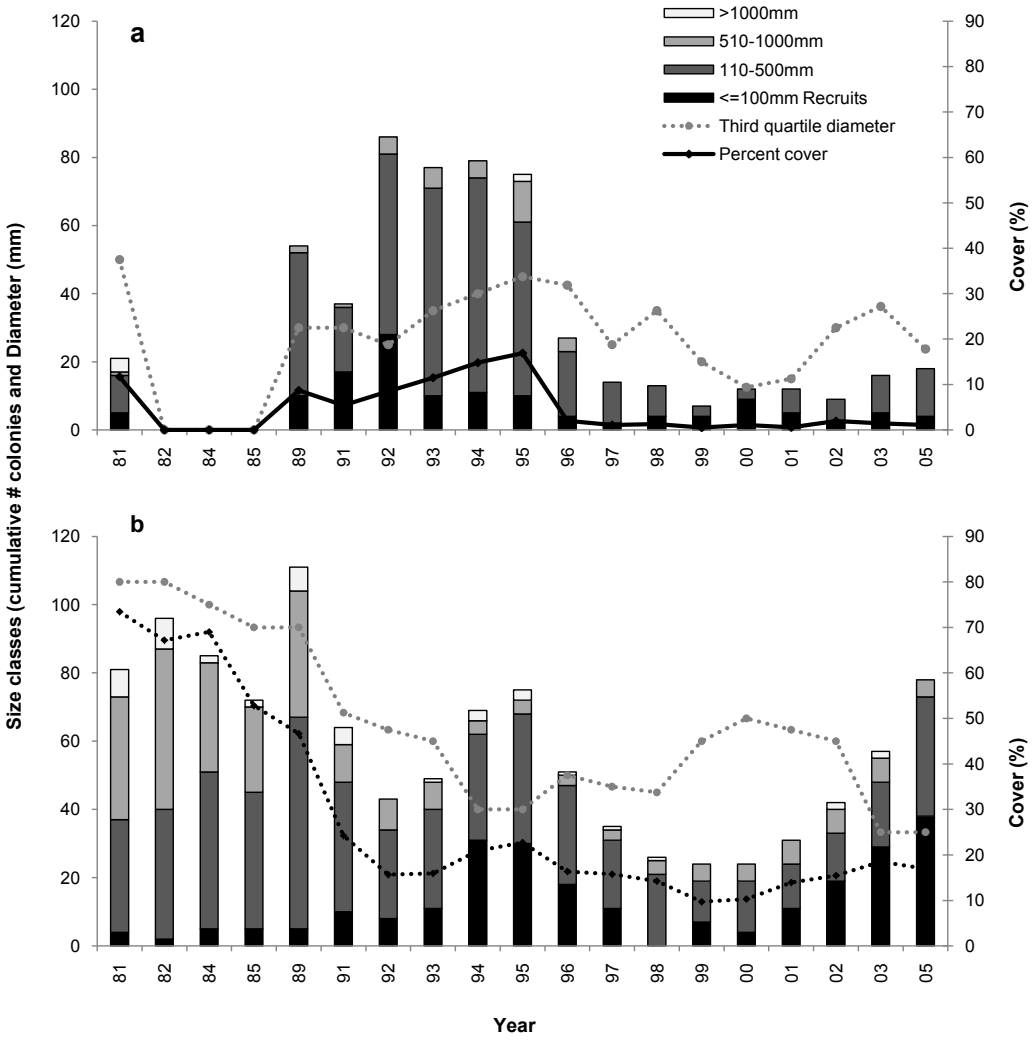


Fig. 3.7 Cumulative size class data, percent cover and third quartile diameter of the *Acropora* plate assemblage through time. **a** South Reef. **b** North Reef.

Discussion

This is one of few studies (e.g. Connell et al. 1997; Done et al. 2007) that have been conducted over a sufficient length of time to address the nature and causes of spatial variability in trajectories of coral composition, abundance, size and cover. The study area - Lizard Island - is in a region where reefs were subject to bleaching, crown-of-thorns starfish and cyclones in recent decades. This study of two sites (each ~ 30 m^2) illustrates how the manifestation of these reef-wide disturbances was highly variable at small spatial scales. We suggest this variability was largely attributable to physical differences between the sites (*viz*. depth, aspect and structural characteristics of the coral assemblage -Fig. 3.3).

Local features determine local dynamics

Adjustment of model parameters to produce a good fit between model projections and observed trajectories proved a useful approach to explore the nature of the differences between these sites, and patch dynamics of coral assemblages in general. Differences in disturbance schedules (mortality probability and patch sizes) more strongly determined assemblage trajectories than differences in growth, recruitment or interaction outcome (see also Wakeford et al. 2008). Thus, while both sites exist putatively within the same regional disturbance regime, the high variability in local assemblages‘ exposure and resistance to disturbance at small spatial scales appears to have been much more responsible for the striking differences between and South Reef and North Reef trajectories. Growth, recruitment and interaction outcomes were overwhelmed by the effects of external forces (storms; crown-of-thorns starfish; bleaching).

Standard monitoring and statistical analysis of coral communities does not capture key attributes that are apparent to observers of natural history traits. For example it was evident at North Reef that the overlapping and fusion of abutting *Acropora* plates confers a strong structural buttressing and resistance to plunging waves at low tides (Fig. 3.2b). This mutual mechanical support among the colonies almost certainly contributed to the slow rate of decline of North Reef‘s *Acropora*

plates in the 1980-90s, despite wave forces that would dislodge individual colonies of the same size attached at a single point (c.f. Madin et al. 2006).

Moreover, their shallowness and resultant occasional exposure of the corals to air during extreme low tides (c.f. continuous immersion of the South Reef coral) might have provided them a degree of resistance to bleaching by pre-selecting for hardy corals able to withstand the elevated heat and sunlight (Brown et al. 2000; Fitt et al. 2001). The occasional sub-aerial exposure and turbulence may also have limited access to crown-of-thorns starfish when they might otherwise have moved from adjacent slopes into the shallows during the 1982 and 1996 outbreaks (Endean and Stablum 1973; Pratchett 2005). However, sustained but patchy coral mortality and dislodgement throughout the 1980s fragmented the formerly consolidated coral structure and probably precipitated the more rapid loss of living and dead colonies after 1990, when cyclone Ivor caused considerable damage to reefs in the vicinity of Lizard Island (Done 1992).

Chronic disturbance as a common feature

Despite clear differences in community dynamics and disturbance schedule, both sites showed signs of a qualitative shift to chronic disturbance around the turn of the century. At both sites, their later years' trajectories of coral cover were reproducible in model projections only by introducing background mortality (Fig. 3.5a, 3.5b), which had not been necessary during previous inter-disturbance periods. The study communities were still recovering from the major 1996 crown-of-thorns starfish outbreak when region-wide mass bleaching occurred in 1998 and 2002 (Berkelmans et al. 2004), and there were also small numbers of crown-of-thorns starfish in and near the site at those times (Sweatman et al. 1998; Pratchett 2005; personal observations). Although a number of corals at the sites partially bleached during both bleaching events (more so at South Reef) there was not a marked increase in coral mortality (i.e. complete colony death). However sub-lethal bleaching can reduce coral growth rates and reproductive output, and increase the incidence of disease (Baird and Marshall 2002; Ward et al. 2002; Harvell et al 2002; Douglas 2003), potentially suppressing regional abundance of viable coral larvae. It is proposed

that since the last crown-of-thorns starfish outbreak there has not been a typical inter-disturbance period with low mortality levels in which coral can fully recover.

In summary, the observations and the modelling provide insights into possible reasons for the failure of these corals to recover in the early years of the 21st century. Both sites appeared to undergo a switch to a more chronic disturbance regime and weaker inter-disturbance recovery. In the context of predictions of _loss' of reefs as a consequence of increasing intensity, frequency and diversity of disturbances associated with global climate change on top of localized pressures, (Hoegh-Guldberg 1999; Kleypas et al. 1999; Wilkinson 1999; Hughes et al. 2003), there is clearly a need for improved understanding of the nature and drivers of patchiness in ecological state, resistance and resilience.

CHAPTER 4

GENERAL DISCUSSION

The complex patterns and dynamics of natural populations reflect the interplay of environment, history of disturbance and the life history traits of component species. Through measurement of demographic rates and understanding of life history strategies, a framework can be built to explain ‗normal' community function, and provide a basis for investigation of processes at different stages of community development. Due to the myriad of processes operating and the complex synergies that arise, small scale and local differences in community configuration can significantly alter dynamics. In this study, an investigation of this type at two coral reef sites at Lizard Island allowed for scrutiny of similarities and differences in community function and local environment, and to highlight their interplay. In particular, the different nature of disturbances and the response of the communities to them were informative regarding aspects of ecological resistance and resilience. In a setting where a changed disturbance regime was implicated by a shift in community structure, the role of seemingly inconsequential processes may have become pivotal (i.e. increased resistance to temperature as a result of exposure during low tide) and conversely, other processes may diminish in importance or no longer occur. The relevance of particular ecological concepts can change significantly.

Because the two study sites were in comparable reef top habits, they supported similar coral assemblages. However there were some important differences in depth and stage of community development, and the 25 year trajectories at the sites were not the same. Demographic rates (recruitment, growth) differed among the two sites, as did the local effects of regional disturbances (mortality and injury from crown-of-thorns starfish, bleaching and cyclones). Spatial differences in effects of disturbance depend not only on local intensity and duration but also, in principle, on the range of life history attributes represented among the resident organisms, e.g. early colonisers and older individuals, and fragile growth forms and strong growth forms, will respond differently to a given disturbance. These attributes, which influence both the robustness (capacity to resist disturbance) and resilience (capacity to recolonise) are closely

linked to species life history. However under changed scenarios (pressures, disturbance regimes) the mix of viable attributes, and thus species, may change.

Community ecology

Findings from this thesis indicate that demographic attributes and inter-specific interactions (mortality, growth, recruitment and outcomes of competition) are not equally important in driving the dynamics of model communities of the two study sites. In all ecosystems recruitment at some stage is fundamental to ensuring long–term persistence of the community (Harrison and Wallace 1990), and competitive interactions can be paramount in determining community structure. However in the models developed here, rates of recruitment and outcomes of competitive interactions between species, even under manipulated scenarios, were not the main drivers of community dynamics.

Recruitment studies at South Reef (E. Turak, unpubl) indicate that coral settlement is extremely variable and unpredictable from year to year. Regardless of the recruitment signal, it is whether a few colonies can establish and grow for 5-10 years that determines whether the community will be maintained. In modelling South Reef, failed recruitment (i.e. zero settlement) did not cause a significant drop in coral cover over the ~20 year time frame modelled, and a ten-fold increase in recruitment did not cause a significant rise over this time. Lack of sensitivity to order of magnitude variability in recruitment reflects the low absolute densities of recruits recorded at the site. An interval of only 7 - 8 years between major disturbances is insufficient time for such a low starting percentage cover contributed by recruits, even multiplied ten times, to make a significant contribution to cover compared to the growth of large established colonies. While it cannot be assumed that this site is generally representative of recruitment rates in this habitat, the study does show that recruitment cannot be taken for granted as a major driver of observed changes over 2-3 decades; it can take a distant third place to survival and growth of established colonies.

As corals establish and grow, their spatial proximity and arrangement has implications for survivorship, interaction and growth. At the early stages of settlement when corals consist of a few flattened polyps multiplying across the substratum to establish a base, competition for space and overgrowth by immediate neighbours can be intense Johnson 1997; Dunstan and Johnson 2003). Once the colony base has established, corals exhibit a vast array of growth forms that allow them to grow into three-dimensional space. Competitive interactions between corals are well documented and play a major role in shaping coral community structure and dynamics (Lang 1973; but c.f. Bradbury and Young 1983). However at the study sites there was no evidence of a clear competitive hierarchy. From year to year, there were reversals in colony overgrowth at their margins, and during periods of high coral cover and limited space many corals touched or overtopped one another. However generally they coexisted without obvious detrimental effects (such as mortality, partial or total) by growing into open space or by existing at different heights above the substratum. Where frequent disturbance created a surfeit of free space, there was a low incidence of competitive interaction before the next disturbance. I conclude that in other habitats with comparable colony sizes and low total coral cover, interactions among established corals and other macro-benthos may similarly be of minor importance; the major drivers of community structure and trajectories seem to be disturbance history and growth (Done et al. 2010).

The study also supports the contention that not all interactions are negative, and that indirect and facilitative interactions are also important in structuring communities (Bruno et al. 2003). In situations of overtopping, particularly by large *Acropora* plates, understory colonies can disappear from plan view for several years and reappear after major disturbances (crown-of-thorns starfish, cyclone) lead to removal of the upper storey. Often, the exposed colony appears healthy although growth tends to be minimal to negligible, especially for faviids and *Porites*. It would not be accurate to imply the upper story affords protection to the understory from disturbance, as the robust form and low palatability of faviids and *Porites* independently gives them heightened resistance to cyclones and crown-of-thorns starfish. However during bleaching events, shading by upper story colonies would reduce levels of irradiance and direct penetration

of light to understorey colonies and similarly during strong waves provide a degree of shelter or buffering to more fragile growth forms. These types of interactions are positive - facilitating better survival rates in both types of colony. In scenarios of increased disturbance frequency and reduced coral cover, competition between colonies for available space or other resources may be reduced, but there also may be a diminution of the beneficial effects of such indirect or facilitative interactions. For example, fission at South Reef by the soft coral *Sarcophyton* spp. was not uncommon and partial mortality to large plates from feeding by crown-of-thorns starfish did result in new colonies re-growing from surviving patches. At North Reef, high cover of plating *Acropora* at the start of the study led to colonies fusing and interlocking, adding strength to the overall structure.

Spatial variability in disturbance

Crown-of-thorns starfish, coral bleaching and cyclones are large scale disturbances that exert considerable impact of mid-shelf reefs of the northern and central Great Barrier Reef (Endean and Cameron 1990; Done 1992; van Woesik et al. 1991; Berkelmans et al. 2004). The two study sites at Lizard Island are putatively exposed to the same regional disturbance regime, but the study showed that the manifestation of the disturbances was highly variable at small spatial scales. At South Reef disturbance events were typically acute, causing significant coral mortality and rapid down-turn in coral cover. This was followed by periods of good coral growth in which cover either regained (post 1982) or exceeded (post 1990) previous levels. In contrast, at the second site (North Reef) disturbance at the start of the study caused a steady decline in coral cover that continued for over a decade. A recovery period (indicated by an increase in hard coral) did not occur until after the impact of Cyclone Ivor in 1990 had caused an even steeper decline in the trajectory of coral cover. The contrast between these sites clearly demonstrated how local factors such as depth, aspect and stage of development of the assemblage (i.e. their cover, size, strength and mutual buttressing) can ameliorate or exacerbate the impact of disturbance.

In chapter three, getting a good fit between observed changes and a modelled trajectory of the coral community at North Reef (shallower, inter-tidal site) required inclusion of site-specific disturbance schedules. It seems likely that at this site, exposure of corals to air during extreme low tides pre-selected for hardy corals able to withstand elevated heat and sunlight (Brown et al. 2000; Fitt et al. 2001), providing them a degree of resistance to the 1982 bleaching event (Harriott 1985). The shallowness of this site also routinely exposed it to high hydrodynamic forces from breaking waves. This has two likely effects on vulnerability, namely the development of more robust and strongly attached corals (individually and in interconnected complexes) capable of better withstanding wave forces that may dislodge corals from the deeper site, and preventing or minimising incursion of crown-of-thorns starfish from the adjacent slopes during the 1982 and 1996 outbreaks on all but very calm days (Endean and Stablum 1973; Pratchett 2005).

Forcing a good fit between model projections and observed trajectories at each site proved useful in explaining the nature of the differences between these sites and providing insight for the more general issue of patch dynamics of coral assemblages. The North Reef community could be modelled adequately using South Reef parameters for growth, recruitment and interaction outcomes coupled with the North Reef disturbance schedule (mortality). This reveals that differences in disturbance schedule between sites, rather than differences in growth, recruitment or interaction outcomes are responsible for driving community dynamics, and that rates of recruitment and interaction outcomes had little influence at these sites (see also Wakeford et al. 2008).

Implications for ecological resistance

It is unreasonable to expect communities on different parts of a reef to respond to disturbance in the same way, or for small sites to represent change at larger scales. As discussed above, local factors appear to be highly influential in driving small scale dynamics. However if several sites (such as the study sites in this thesis) in similar habitats but with dissimilar disturbance histories nonetheless all show evidence of a change in ‗normal' system structure around the same time,

then this is likely to point towards a fundamental shift in dynamics or loss of resilience overall. In our study, we would not expect that communities at two sites on the reef, with different initial community structure and disturbance schedules, would have similar trajectories. However, if a model that accurately predicts the different trajectories based on the same kinds of processes (disturbance history, growth, recruitment, and interaction outcomes) ceases to predict well at the same time at both sites, this may reflect that some other larger scale process is in effect. The results presented here suggest a qualitative switch from acute to chronic disturbance around the turn of the century.

This shift was characterised by elevated background rates of mortality during periods between disturbances, and a failure of *Acropora* plates to re-establish. At both sites these low, flattened trajectories were reproducible in model projections only by introducing background mortality, (attributable in the field to crown-of-thorns starfish and bleaching). Moreover, sub-lethal bleaching can depress recovery by reducing coral growth and reproductive output, increasing the incidence of disease, and elevating mortality rates (Baird and Marshall 2002; Harvell et al. 2002; Ward et al. 2002; Douglas 2003; Ainsworth et al. 2007; Rosenberg et al. 2007). Field observations late in the study were inconclusive in relation to this possibility. From 2001 onwards, the shallower North Reef did, in fact, receive good numbers of *Acropora* plate recruits and combined with high growth rates in this species provides a promising basis for resurgences to former levels of dominance by this species. However in the last sample (2005), there was elevated coral mortality (a few colonies had completely gone and a few others were dead standing). Future observations of these sites are necessary to test the hypothesis of a fundamental shift in community dynamics. A third site in the vicinity of North Reef (shallower and more protected) supports a coral assemblage dominated by encrusting *Montipora* spp. (average cover 22 %) with low level contributions from *Acropora* ‗corymbose', *Acropora* plates, *P. damicornis*, faviids and the soft coral, *Sinularia* spp. (average cover about 2% each). Preliminary analysis shows that although cover of encrusting *Montipora* spp. fluctuated over the 25 year study period, it supported a very similar cover in 2005 as in 1981 (~ 25 %). The other corals had fairly flat trajectories throughout, apart from *Acropora* ‗corymbose' and *Acropora* plates, which showed

good coral growth from 1991 -1995 and reached their highest cover in 1995 (7-8%). Both these corals declined rapidly from 1996 and although *Acropora* ‗corymbose' finished with a similar cover in 2005 to that in 1981, *Acropora* plates were reduced to zero cover by 1997 and never regained a presence. These preliminary results suggest that the dominant coral, encrusting *Monitpora*, differs in its vulnerability to events that have driven change in the disturbance regime at North Reef and South Reef. However, the vulnerability of *Acropora* plates at this site from 1997 was consistent with the trajectories of this group at North Reef and South Reef (where it was the dominant coral group).

Future predictions

Future predictions for the state of coral reefs are dire (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007; Veron 2008). Decreased in aragonite saturation and increases in disturbance frequency suggest the persistence of coral reefs in their current form in many parts of the world is unlikely. This study provided a concrete example of how important the frequency of disturbance can be in shaping community structure (see also Done 1987; 1988). Whereas a major disturbance event modelled every 16 years produced a community that rapidly becomes dominated by plating *Acropora* (97%), disturbance at a frequency of every two years led to a community that no longer supported hard coral and where only low levels of soft corals persisted. The optimal disturbance interval was 8 years, repeatedly regenerating the mixed hard coral dominance observed at South Reef in the 1980s and 1990s.

Being able to reliably predict a range of possible scenarios (responses) to disturbance is fundamental to redefining reasonable expectations for the community structure of coral reefs in coming decades. Determining when a change is the result of a fundamental shift in underlying dynamics (Rand and Wilson 1995; Johnson 2009) and what the underlying causes may be (e.g. Underwood 1994) are challenging but pertinent issues for both ecologists and managers (Johnson 2009). Dramatic shifts have been documented for a range of ecosystems (Scheffer and Carpenter 2003), frequently triggered by the occurrence of large external impacts (e.g. cyclones) that are rare at a given place within most human observation scales. However, small incremental change

in conditions can also trigger large shifts in some systems. This implies that gradual changes, such as in temperature, may have little effect until a threshold is reached, at which stage a large shift occurs that might be difficult to reverse (Scheffer and Carpenter 2003). These authors note that to effectively detect shifts in ecosystems, it is essential that theory be linked to observation through research that is a combination of field observations, experiments and models. In as much as the contrasting sites impacted by disturbances are ‗natural experiments', this study meets these key elements

One important goal in ecology is to determine the optimum scale and duration at which to monitor a system, if trying to detect the mechanisms that generate patterns (Carlile et al. 1989; Levin 1992; Habeeb et al. 2005, 2007). The quarter of a century covered by the present study has clearly proven useful in this regard – allowing trajectories to be followed in the face of several disturbances of different types, and several intervening periods for recovery. Like studies aimed at determining the characteristic length scale of ecosystems (Keeling et al. 1997; Pascal and Levin 1999; Habeeb et al. 2007) the present study provided a record and analysis of temporal change in community structure of sufficient detail to suggest there may have been a fundamental shift in underlying dynamics (Wakeford et al. 2008). However even in supposedly well understood ecosystems, there are often still unforseen dramatic shifts, and it is not until after the event that the probable underlying mechanisms are unravelled (Scheffer and Carpenter 2003). Clearly, further long term studies of coral communities in a wide range of habitats will heighten insight and predictive capability.

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